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A FORMAL ANALYSIS OF PHYLOGENETIC TERMINOLOGY: TOWARDS A RECONSIDERATION OF THE CURRENT PARADIGM IN SYSTEMATICS

DAMIEN AUBERT
Ministère de l'Éducation Nationale, Académie de Clermont-Ferrand
Rectorat 3 Avenue Vercingétorix 63033 Clermont-Ferrand cedex 1 France
damien.aubert@ac-clermont.fr

ABSTRACT

BACKGROUND: For too many years the practice of systematics has been impeded by profound disagreements about the very foundations of this discipline, that is to say the type of information that should or should not be incorporated into a proper classification of life. Two main schools of systematics, both recognizing evolution, oppose each other: cladism states that the classification should only reflect the branching order of the lineages on the tree of life whereas evolutionism states that the length of the branches, that is the degree of modification, should also be taken into account so as to reflect macroevolutionary leaps. The first one forbids the exclusion of any descendant from a group that contain its ancestors, while the second one explicitly requires that the descendants too much different from their ancestors must be classified separately. Moreover, both schools often use the same words, such as "monophyly," to designate different ideas. This prevents proper communication between the proponents of either side. Consequently, the research in phylogenetics is globally erratic and the taxonomic classification is highly unstable.

RESULTS: I rigorously define the terms which designate the phyletic relationships and explore their properties through use of graph theory. I criticize a similar work (Kwok 2011) that was unable to properly catch these notions. This leads me to provide three independent arguments — one historical, one utilitarian, and one morphosemantic — in order to retain the original Haeckelian meaning of the term "monophyly" rather than the redefined Hennigian one. I identify some polysemy regarding the term "clade," and that is why I define two new words, "holoclady" and "heteroclady," to contrast respectively with "holophyly" and "heterophyly." I also show that a strictly holocladic or holophyletic classification advocated by cladists is formally impossible. I therefore review and criticize the philosophical postulates subtending such an illogical paradigm. I show that cladism is part of a more general philosophical movement named structuralism, which is mainly characterized by anti-realism and a metaphysical way of thinking. I identify the biologically unrealistic assumptions on which cladism is based and argue that they have been empirically falsified. I therefore defend the use of paraphyletic groups in the scientific classification of life and review the main arguments that have been opposed to this solution. Some of them, such as anthropocentrism or the lack of an objective manner to determine paraphyletic groups, are grossly outdated, while others simply rest upon the difficulty in conceptualizing emergent phenomena.

CONCLUSION: Since clades are still useful for methodological reasons, I offer a compromise that should make possible the coexistence of the two main opposing schools of systematics by eliminating competition between clades and taxa for the same names. I propose therefore that in a future revision, the *BioCode* should approve a dual system by recognizing both a "phyletic arrangement" made of clades and a "phylogenetic classification" made of taxa.

"We often discussed his notions on objective reality. I recall that during one walk Einstein suddenly stopped, turned to me and asked whether I really believed that the moon exists only when I look at it." (Pais 1979)

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INTRODUCTION

Systematics has been marked for many decades by vigorous methodological debates concerning the classification of life, especially regarding the status of paraphyletic groups (Mayr 1974; Hennig 1975). These debates have annoyingly never reached a true consensus (Mayr & Bock 2002; Goldenfeld & Woese 2007). These disputes about the topological properties of taxa were interspersed with major terminological controversies (Ashlock 1971; Nelson 1971; Ashlock 1972; Nelson 1973) which plagued the discussions, even today blurring practice and progress in this discipline (Brummitt 1997; Cavalier-Smith 1998; Mayr 1998; Woese 1998; Ghiselin 2004; Brummitt 2006; Hörandl 2007; Podani 2010b; Zander 2011; Schmidt-Lebuhn 2012; Schmidt-Lebuhn 2014; Stuessy & Hörandl 2014; Brummitt 2014).

Although both opposing sides have firmly stood their ground over the years, one quickly took the ascendancy over the other in both practice (Dumoulin & Ollivier 2013) and teaching (Lecointre et al. 2008) of systematics throughout the world. This relatively recent paradigm, which is called "cladism", insists on the purely "genealogical" pattern that a natural classification of living things must have. According to it, taxa must be delimited through a unique formal principle: the inclusion of all descendants of the last common ancestor of its members (Hennig 1966). Cladism probably owes its success in part to the attractiveness of this imperative which is supposed to facilitate the decision making process and free the classification of life from all forms of subjectivity (Hennig 1966; Hennig 1975; Schmidt-Lebuhn 2012). Cladism unfortunately appeared in conjunction with a new method of resolving phyletic relationships: cladistics (Hennig 1950; Hennig 1966). Always presenting themselves as inseparably linked to each other, up to using the same word of "cladistics" to refer to one or the other (Ashlock 1974; Mayr 1974; Hennig 1975), cladism directly benefited from

the popularity and effectiveness of this method. The opposing position, evolutionism, has therefore been described as "traditional" or "classical" to emphasize its purported obsolescence. Rejecting cladism would therefore be a synonym of rejecting cladistics, and therefore rejecting progress (Hennig 1975). This claim does not give a faithful image of modern evolutionary systematics which has fully integrated the contributions of cladistics and of subsequent molecular phylogenetic techniques to give birth to many fertile theories (Cavalier-Smith 2002a; Cavalier-Smith 2010a; Zander 2013).

The purpose of this paper is primarily to rigorously analyse, with the aid of an appropriate mathematical formalism, the notions of systematics in order to objectively solve the terminological dispute which has been plaguing the theoretical discussions for half a century. On the basis of this common vocabulary, I intend on the one hand to reveal some logical inconsistencies arising from cladism, and on the other hand to decipher the philosophical foundations that underlie them. This will allow me to resolutely advocate abandoning sterile cladism and rallying evolutionary systematics. However, I will also propose a short-term workable compromise which would allow the establishment of a "peaceful coexistence," or even cooperation, between practitioners of cladonomy and those of taxonomy.

1. GENEALOGICAL NETWORKS

It is not the first time that one tries to formally define the phylogenetic concepts. Hennig himself modelled the succession of generations in sexual populations through directed acyclic graphs (Hennig 1966). However Kwok (2011) pointed out that "[w]here mathematical definitions have been presented [...], the properties of such concepts have not been explored". This fact greatly limited their usefulness. Such an exploration was recently attempted (Kwok 2011), but it failed to adequately describe some key concepts because of the choice of bad axioms as I shall demonstrate. Curiously, the author nonetheless came to the same conclusion as I, concerning the impossibility of consistently reconciling the Linnaean hierarchy with cladism, but without realizing all the implications. In the course of this work, I will therefore emphasize the reasons justifying the better adequacy of my model to the biological reality. I will also insist on the logical consequences that prove the unreasonableness of the cladist imperative and of the assumptions that constitute its framework of thinking. Since this paper focuses on definitions and terminology, and does not have the ambition to unveil novel mathematical properties of directed acyclic graphs, I have relegated in the annexe the proofs of the various lemmas and theorems.

Definition 1.1 *(Genealogical Network)* A genealogical network G is a pair (X, p) where X is a non-empty finite set and p is a binary relation on X such that p is acyclic, i.e. for every sequence x_1, x_2, …, x_n of elements of X, if $n \geq 2$ and if for every i, $1 \leq i \leq n-1$, $(x_i, x_{i+1}) \in p$, then $x_1 \neq x_n$.

This definition of a genealogical network matches the one of a *directed acyclic graph* (or DAG), a common mathematical object in graph theory. As a consequence of this definition, it can be trivially drawn that $(x, x) \notin p$ for every $x \in X$. The set X embodies a population and the pair $(x_1, x_2) \in p$ should be read as "x_1 is a parent of x_2" (see Figure 1).

Definition 1.2 *(Lineage)* Let there be a genealogical network $G = (X, p)$. A sequence x_1, x_2, …, x_n of elements of X is called a lineage if $n = 1$, or else if $n \geq 2$ and $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq n-1$.

In particular, for any $x \in X$, the sequence consisting of the single element x is a lineage. Intuitively, a lineage is thus a line of descendants without gaps.

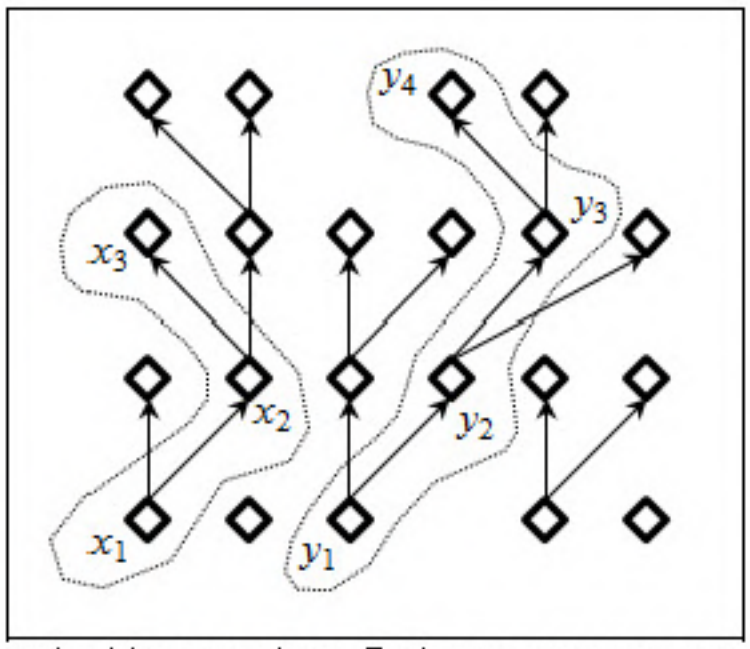

Figure 1. A genealogical network without mergings. Each square represents an individual. The whole of the squares constitute the set X. The whole of the arrows represents the binary relation p defined on the set X (every arrow is an element of p). For example, x_1 and y_4 are individuals. The individual x_1 is a parent of x_2 (see Definition 1.1). The sequence x_1, x_2, x_3 is a lineage (see Definition 1.2) and x_1 is an ancestor of x_3 (see Definition 1.3), but x_3 is not an ancestor of x_1 (see Lemma 1.6). The individual y_1 is an ancestor of y_2 which is itself an ancestor of y_4, therefore y_1 is an ancestor of y_4 (see Lemma 1.5).

Definition 1.3 *(Ancestor)* Let there be a genealogical network $G = (X, p)$ and $x \in X$. An individual $a \in X$ is an ancestor of x if and only if there exists a lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$ and $x_n = x$.

Observation 1.4 Let there be a genealogical network $G = (X, p)$, whatever $x \in X$, x is an ancestor of x.

This observation, although counter-intuitive, is a trivial consequence of Definition 1.2 and Definition 1.3. Kwok (2011) correctly noted that this property greatly facilitates the formulation of many propositions thereafter. This fact has been longstandingly remarked, for example by Ashlock (1972) who noticed, following Tuomikoski (1967), that "Hennig's definition of monophyly—all descendants of the most recent common ancestor—specifically excludes the stem ancestor of the group, *since the stem ancestor cannot be descendant of itself* [my emphasis]." The choice we make therefore simplifies our wording without falling into such a trivial trap. The following lemmas collect some well-known facts about DAGs.

Lemma 1.5 *(Transitivity)* Let there be a genealogical network $G = (X, p)$ and three distinct individuals $a, b, c \in X$. If a is an ancestor of b and b is an ancestor of c then a is an ancestor of c.

This is of course true in the special case where $(b, c) \in p$, i.e. $k = n + 1$.

Lemma 1.6 *(Non-Reciprocity)* Let there be a genealogical network $G = (X, p)$ and $x, y \in X$ such that $x \neq y$, if y is an ancestor of x then x is not an ancestor of y.

Lemma 1.7 *(Fragmentation of a Lineage)* Let there be a genealogical network $G = (X, p)$, g a non-empty subset of X, and the individuals $a \in g$ and $x \notin g$. If a is an ancestor of x, then for every lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$ and $x_n = x$, it exists a certain i, $1 \leq i \leq n - 1$, such that $x_i \in g$ and $x_{i+1} \notin g$.

Figure 2 exemplifies Lemma 1.7. Following the everyday terminology of biologists, I will thereafter use the term "group" to refer to any non-empty subset g of X.

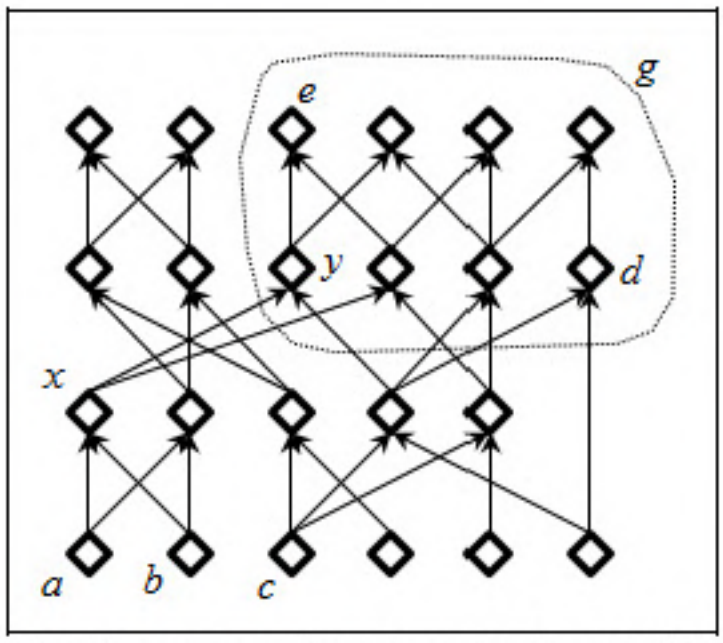

Figure 2. A genealogical network with mergings. In such a network, an individual x could be descended from parents a and b for example. A parent, like c, can reproduce with different partners. Some individuals, like d, can be descended from parents of different generations. In this example a is an ancestor of e which belongs to an arbitrary group g. The individual a therefore belongs to a group g', complementary to g in X, to which e does not belong. By Lemma 1.7 it exists therefore an individual x not belonging to g which is a parent of an individual y belonging to g.

Definition 1.8 *(Subnetwork)* Let there be a genealogical network $G = (X, p)$ and a group $g \subset X$. Let us say that $G' = (X', p')$ is a subnetwork of G generated by g if and only if $X' = g$ and $p' = p \cap g^2$.

This definition allows us to trivially convert a group into a subnetwork, thus permitting us to simply extend group properties to networks.

Definition 1.9 *(Group without Mergings)* Let there be a genealogical network $G = (X, p)$ and a group $g \subset X$. Let us say that g is a group without mergings if and only if no organism in g has multiple parents.

Observation 1.10 *(Network without Mergings)* Let there be a genealogical network $G = (X, p)$, a group $g \subset X$ and G' a subnetwork generated by g. If g is a group without mergings then G' can also be called a network without mergings.

The converse of this definition does not hold inasmuch as an element of a network without mergings can accept several parents provided that they are not members of it. A network without mergings can be called a "tree". It is not necessarily dichotomous. It is however the most common case because of the binary fission of prokaryotes or the eukaryotic mitosis. The absence of mergings of different lineages implies the absence of sexuality, the absence of hybridization and the absence of symbiogenesis.

Lemma 1.11 *(Uniqueness of a Lineage)* Let there be a genealogical network $G = (X, p)$ without mergings and the individuals $a, x \in X$. If a is an ancestor of x then it does exist only one lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$ and $x_n = x$.

Theorem 1.12 *(Relation between Ancestors)* Let there be a genealogical network $G = (X, p)$ without mergings and the individuals $a, b, x, y \in X$. If a is an ancestor of x and y, and b is an ancestor of x but not of y, then a is ancestor of b.

The properties expressed by Lemma 1.11 and Theorem 1.12 are depicted in Figure 3. These preliminary definitions being established, we now have the necessary materials to tackle the problem of monophyly.

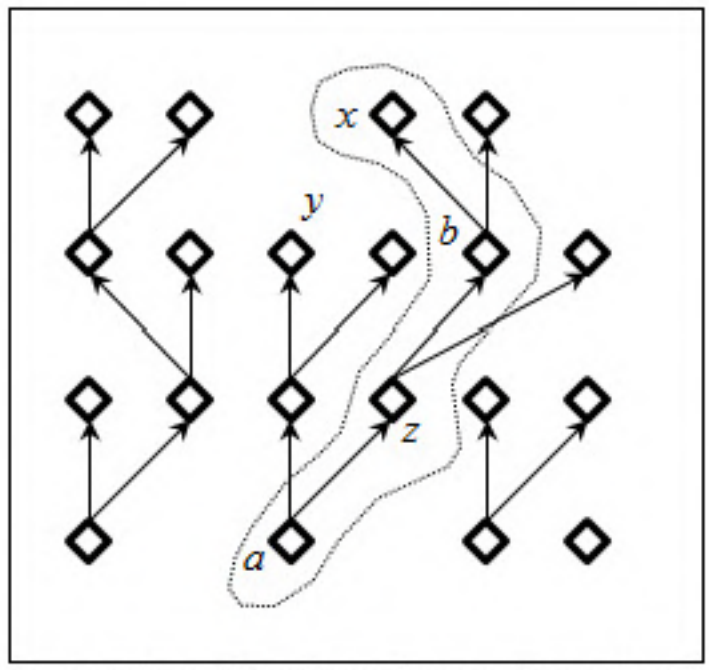

Figure 3. Relations between the ancestors of a unique lineage in a network without mergings. Since this genealogical network is without mergings and a is an ancestor of x, then by Lemma 1.11 there exists only one lineage linking these two individuals: a, z, b, x. In the same way, since a is an ancestor of both x and y whereas b is an ancestor of x only, we conclude by Theorem 2.12 that a is an ancestor of b. If we define $g = \{x, y\}$ then a is a common ancestor of g (see Definition 2.1).

2. COMMON ANCESTORS AND MONOPHYLY

It is remarkable how such a central concept like monophyly in a discipline like systematics fails to be unanimously defined. This paradox may be due in part to the fact that despite awkward definitions, the claim that a group must be monophyletic in order to be considered a taxon, i.e. a natural group, was already consensual before cladism has imposed itself. We found for example in Simpson (1961) a wording which seems today rather obscure: "monophyly is the derivation of a taxon through one or more lineages from one immediately ancestral taxon of the same or lower rank".

Taking advantage of these awkwardnesses, it was easier to make cladism acceptable by subtly redefining the concept of monophyly rather than defining a new concept that would have had to impose itself by replacing the former. Thus, Hennig (1950; 1966) just had to claim to formulate a more precise definition while expropriating it (Ashlock 1971; Ashlock 1972; Mayr 1974; Mayr & Bock 2002). Today the most widespread definitions are similar to those of Hennig. But If we go back to the roots, the word "monophyletic" was originally coined by Haeckel (1866) to refer to the theory that all extant organisms are descended from a single common ancestor, i.e. that life has appeared only once. Its use was later extended by its inventor himself to describe the taxa (or "phyla" in his terminology) of a natural classification of life:

"*Unter Phylon verstehen wir stets die Gesammtheit aller blutsverwandten Organismen, die von einer gemeinsamen typischen Stammform abstammen.*" (Haeckel 1877)

By phylon we invariably understand the totality of the organisms related by blood, descended from a common *typical* ancestor [my translation and my emphasis].

The adjective "typical" allows Haeckel to exclude divergent descendants who do not share the ancestral body plan, thus creating valid monophyletic groups like Reptilia (the reptiles) whereas some descendants like Aves (the birds) are deliberately removed (Haeckel 1868). The addition of this very word in the third edition of his *Anthropogenie* demonstrates the lucidity of Haeckel regarding the inadequacy and awkwardness of the definition he had originally given in the first edition of his book (Haeckel 1874). As we can clearly see, the concept of monophyly is centered on the ancestor, and more precisely the unique ancestor (which justifies the choice of μόνος "alone" in its etymology), not on the descendants! Thus, in his analysis of Haeckel's terminology, Dayrat (2003) notes: "In the two words 'monophyletic' and 'polyphyletic,' [the etymon *phylon*] clearly refers to the concept of stem."

The historical fact that Hennig had actually redefined the concept of monophyly by significantly straying from its Haeckelian use seems today to be tacitly accepted by some cladists (Vanderlaan et al. 2013). We shall see later other reasons not to retain the Hennigian meaning (see Section 4 and Section 5). But first let us begin by defining hereinbelow the notion of common ancestry, and then use it so as to rigorously formulate the concept of monophyly *sensu* Haeckel.

Definition 2.1 *(Common Ancestor)* Let there be a group g and an individual $a \in X$, a is a common ancestor of g if and only if for every $x \in g$, a is an ancestor x.

In particular, and as a consequence of Observation 1.4, for every $x \in X$, x is a trivial common ancestor of the group $\{x\}$.

Definition 2.2 *(Most Recent Common Ancestor)* Let there be a group g and $a \in X$ a common ancestor of g. The individual a is a most recent common ancestor of g if and only if for every a' common ancestor of g, either a is not an ancestor of a', or else $a = a'$.

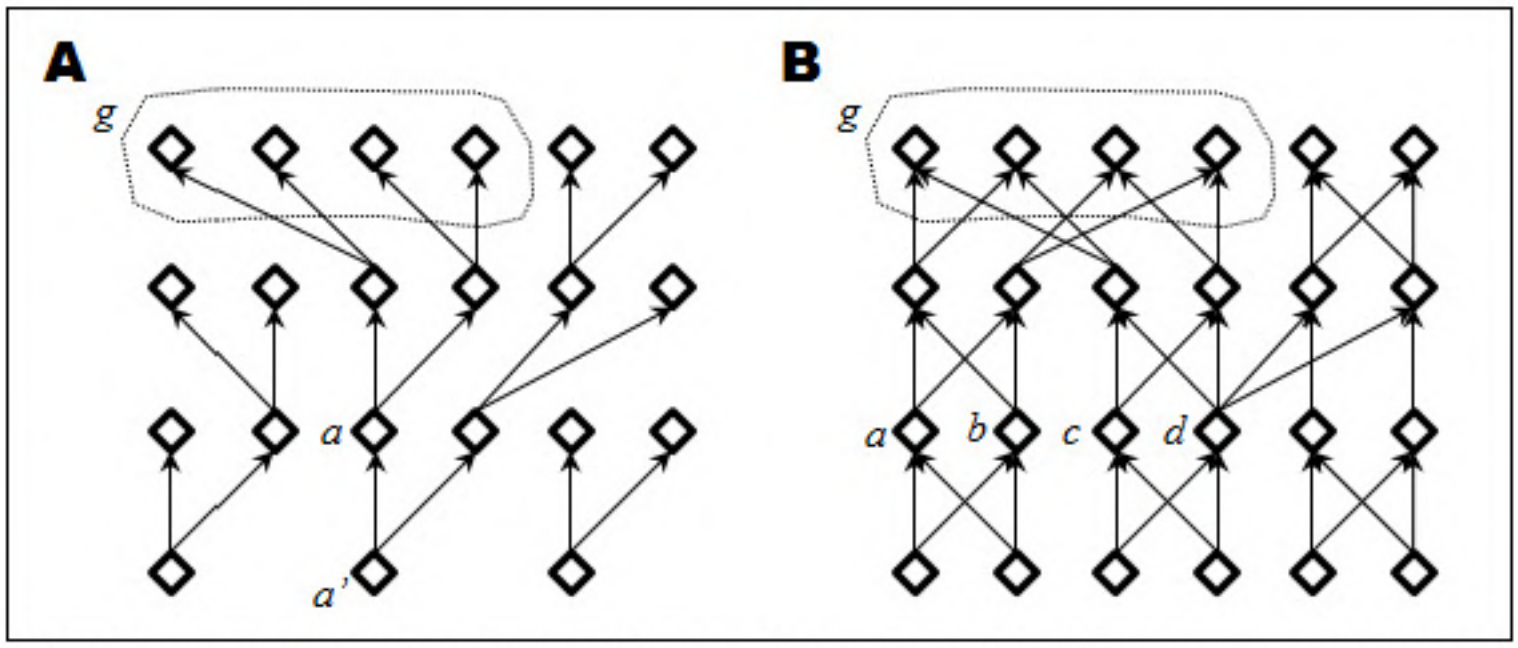

Figure 4. Common ancestors in networks without or with mergings. (A) a' is a common ancestor of g but is not a most recent common ancestor of g because it is itself an ancestor of a which is also a common ancestor of g. The individual a is on the contrary a most recent common ancestor (cenancestor) of g because it does not exist descendants of a that are common ancestors of g. (B) In the framework of sexual reproduction, a, b, c and d are equally in this example the four most recent common ancestors (cenancestors) of g.

A most recent common ancestor does neither necessarily belong to g, nor is necessarily unique, as for example in the case of sexual reproduction (see Figure 4). A most recent common ancestor is sometimes called a cenancestor in evolutionary biology, with a prefix "cen-" derived from both καινός "recent" and κοινός "common". The concept of cenancestor was originally used in the more restricted meaning of last universal common ancestor (Fitch & Upper 1987; Doolittle & Brown

1994; Cavalier-Smith 2001), but it is as such a too narrowly defined term for an ordinary use in everyday systematics, i.e. outside the very specific field of the origin of life. It can be indeed observed that in other contexts the few authors that use this term tend to talk about the cenancestor of either this or that group (Cavalier-Smith 2002a). The others use acronyms (Koonin 2010; Valas & Bourne 2011) such as LECA (last eukaryotic common ancestor), LACA (last archaebacterial common ancestor), etc. or else give some special names to these common ancestors, like "urbilateria" (Moroz 2012; Nilsson 2013) which derive from the taxon's name Bilateria and from the German prefix "ur-" which marks an origin. This lack of homogeneity in scientific literature could be easily resolved by the regular use of the word cenancestor in the broad sense: it has the advantages of being simple, transparent and readily adaptable to any situation.

Definition 2.3 *(Monophyletic Group)* Let there be a group g, g is said to be monophyletic if and only if there exists $a \in g$ such that a is a common ancestor of g.

Lemma 2.4 *(Uniqueness of the Included Common Ancestor)* For any monophyletic group g, there exists only one common ancestor a of g such that $a \in g$. This unique included common ancestor is also a most recent common ancestor (cenancestor) of g.

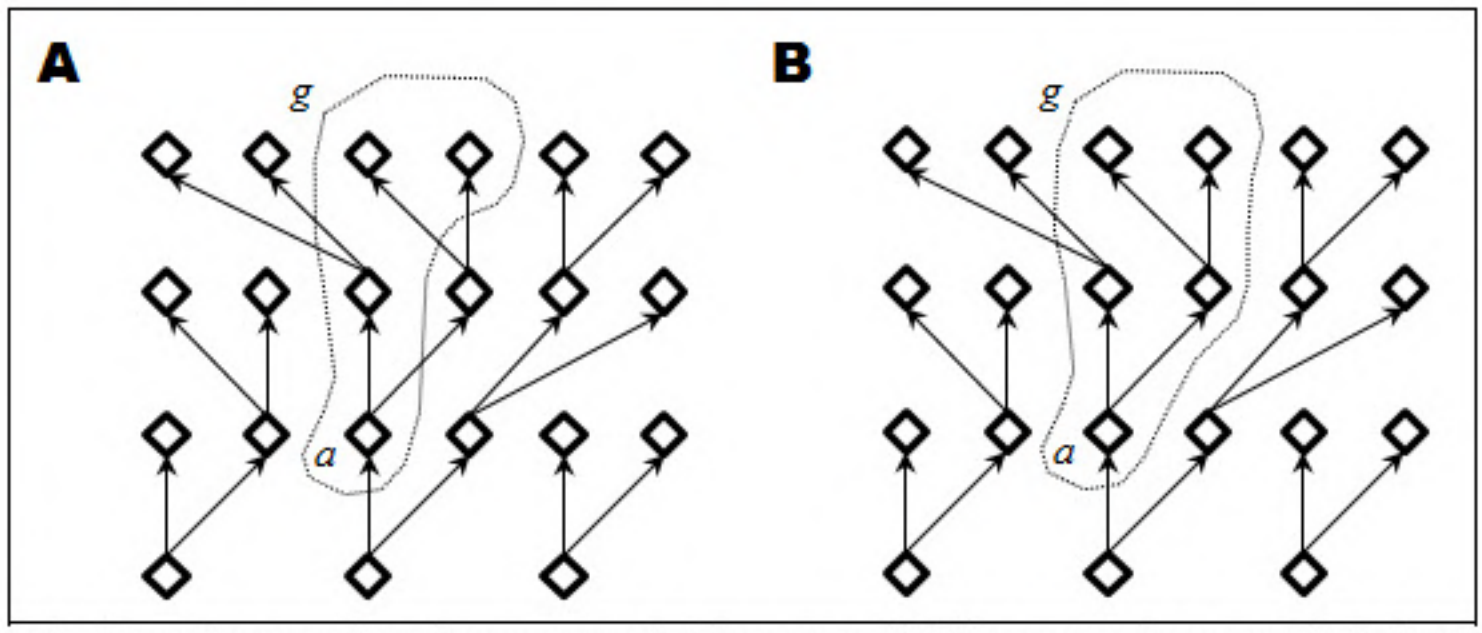

Figure 5. Discontinuous and continuous monophyletic groups. (A) The group g is monophyletic because a, which belongs to g, is an ancestor of all the members of g. (B) The group g is monophyletic and continuous because for all the members of g there exists at least one lineage linking them to a such that all the members of these lineages belong to g.

This first definition of monophyly means that a group can only be considered as such if it is formed of descendants of one of its members. The problem that this simple formulation poses is that the intermediate individuals linking a cenancestor to the other members of the group are not necessarily themselves members of this very group (see Figure 5A), which is obviously at odds with the spontaneous idea that biologists have of monophyly. This logically leads us to add a condition of lineage continuity so that the properties of our formal definition match those of real biological groups studied in practice (see Figure 5B).

Definition 2.5 *(Continuous Monophyletic Group)* Let there be a monophyletic group g and a its unique included common ancestor. The group g is said to be continuous if and only if for every $x \in g$ there exists at least one lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$, $x_n = x$, and if $n > 1$ then $x_i \in g$ and $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq n-1$.

A "continuous monophyletic group" can simply be called a "continuous group". A monophyletic group that is not continuous can unequivocally be called "discontinuous". As we can see, our wording is centred on the ancestor. Conversely, Kwok (2011) focuses on descendants. He begins by defining a "descent group" as comprising a set of progenitors and all of their descendants (his Definition 3). Next, he specifies that two descent groups are "disconnected" if their intersection is the empty set (his Observation 14). This finally allows him to define a monophyletic group as being a descent group that cannot be split into two disconnected descent groups (his Definition 15).

The main flaw of his definition is not the inclusion of all the descendants of the progenitors, but the non-uniqueness of these progenitors (see Lemma 2.4). As we can see in Figure 6A the connected descent groups do not necessarily correspond to monophyletic groups by our definition since they do not always contain a unique most recent common ancestor! The goal of this author was to find out a way to link together genealogy and phylogeny. He thus started from the biased assumption that what occurs in infraspecific and supraspecific levels is fundamentally different (which we shall refute later, see Theorem 6.2). He seems to have been abused by the so-called "biological definition" of a species, i.e. as a group of interbreeding individuals. However, sexuality is only an epiphenomenon, proper to the eukaryotes alone in the entire living world. Life did have only prokaryotic asexual reproduction for at least its first two billion years of existence (Cavalier-Smith 2002b; Gross & Bhattacharya 2010; Cavalier-Smith 2010b). This led him to ignore the definitions of monophyly on which he did rely so far: "an ancestor and all of its descendants" (Barton et al. 2007). It should also be noted that the merging of two lineages is not an exclusive phenomenon of sexuality, it is found for example in hybridization between two closely related species (furthermore fairly common in plants) or in symbiogenesis between two very distant species. Although these events are rarer it would be unacceptable to exclude them from our model. Their consideration renders the shortcomings of Kwok's definition (2011) especially flagrant (see Figure 6B). Treating species like any other taxon is actually the most parsimonious solution in terms of hypotheses. The next parts of our study should enable us to move from this base taxon to higher taxa while maintaining the consistency of the already studied topological properties. The two following lemmas are very well-known properties about trees it is worth mentioning.

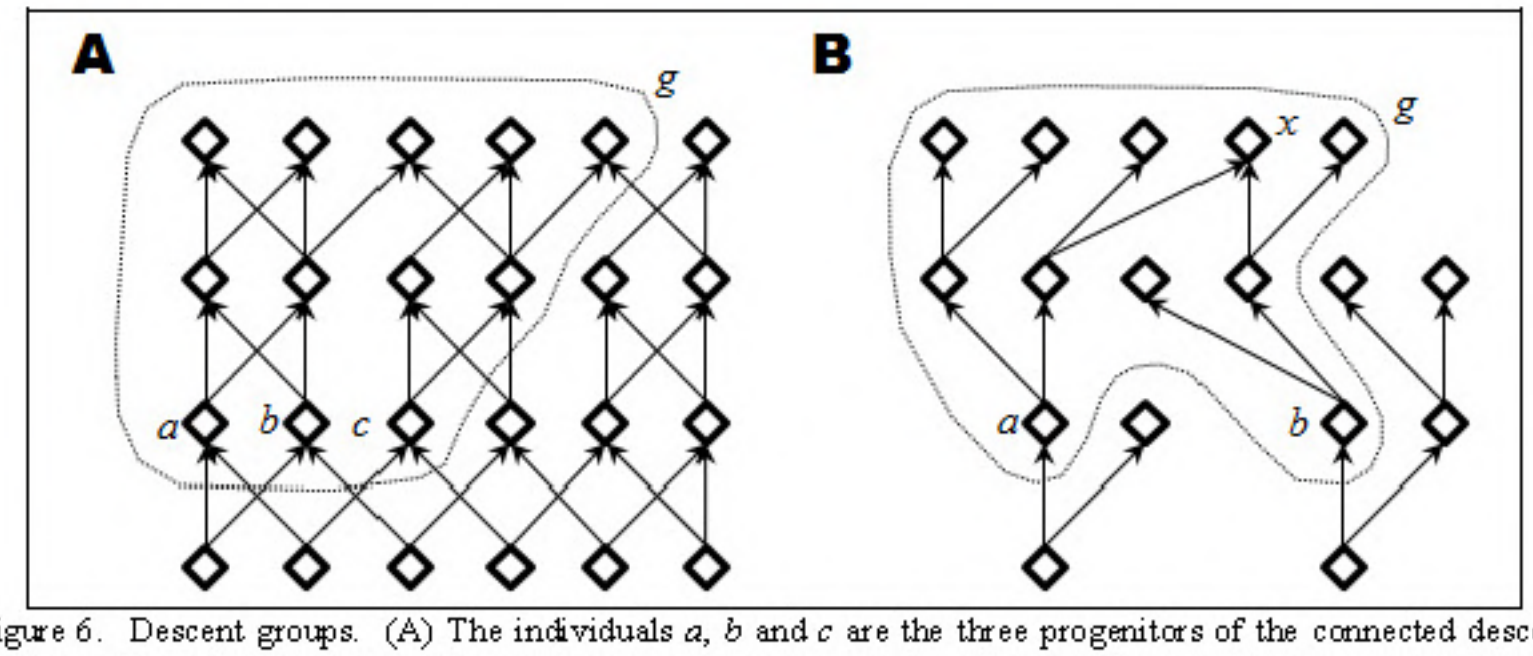

Figure 6. Descent groups. (A) The individuals *a*, *b* and *c* are the three progenitors of the connected descent group *g*. Since it does not contain a unique common ancestor, then it cannot be considered as monophyletic. (B) The individuals *a* and *b* are two progenitors of the connected descent group *g*. We can imagine for example that *a* is the most recent common ancestor of all protozoa and *b* the one of cyanobacteria, such that *x* is the one of plants. It would be of course absurd to consider the set "protozoa + cyanobacteria + plants" as monophyletic.

Lemma 2.6 *(Uniqueness of the Lineages in Continuous Groups without Mergings)* Let there be g a continuous monophyletic group defined in a genealogical network without mergings $G = (X, p)$, and the individuals a, $x \in g$ such that a is an ancestor of x. Then it does exist only one lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$ and $x_n = x$. Moreover, $x_i \in g$ for every i, $1 \leq i \leq n$.

Lemma 2.7 *(Uniqueness of the Most Recent Common Ancestor)* Let there be a genealogical network without mergings $G = (X, p)$, a group $g \subset X$ and $a \in X$ a most recent common ancestor (cenancestor) of g. Then there does not exist $a' \in X$ being a most recent common ancestor of g such that $a \neq a'$.

3. ANCESTRAL GROUPS AND MONOPHYLETIC UNIONS

We studied as a first step the relations between individuals. In order to generalize these properties to groups of individuals we must expand our definitions to group relations.

Definition 3.1 *(Ancestral Group)* Let there be g_1 and g_2 two monophyletic groups such that $g_1 \cap g_2 = \emptyset$, and a the unique included common ancestor of g_2. We can say that g_1 is an ancestral group of g_2 (or that g_1 is ancestral to g_2) if and only if there exists $x \in g_1$ such that x is an ancestor of a.

Definition 3.2 *(Directly Ancestral Group)* Let there be g_1 and g_2 two monophyletic groups such that $g_1 \cap g_2 = \emptyset$, and a the unique included common ancestor of g_2. We can say that g_1 is a directly ancestral group of g_2 (or that g_1 is directly ancestral to g_2) if and only if there exist $x \in g_1$ such that $(x, a) \in p$.

Ancestral groups are clearly analogous to ancestors of individuals (see Figure 7A). Likewise, directly ancestral groups can be regarded as equivalent to parents of individuals. Incidentally, it is not rare to find in scientific literature phrases like "sister group" or "daughter group" to characterize such relationships (see Figure 7B). Thus we can say that Reptilia is the mother group of Aves and Mammalia, which are its two daughter groups.

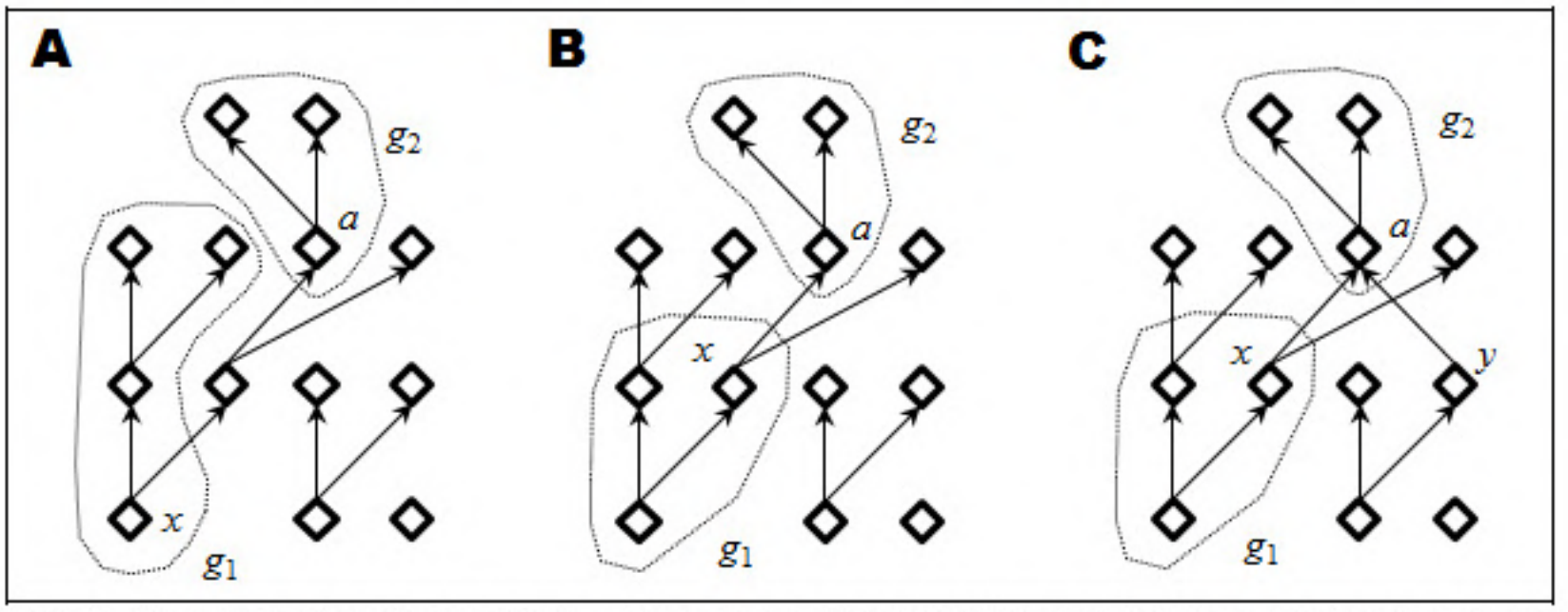

Figure 7. Typology of ancestral groups. (A) g_1 is a group indirectly ancestral to g_2 because $x \in g_1$ is an ancestor of a, itself the last included common ancestor of g_2, but there does not exist an individual of g_1 that a parent of a. (B) g_1 is here directly ancestral to g_2 because $x \in g_1$ is a parent of a; it is also a group exclusively ancestral to g_2 because all the parents of a belong to g_1. (C) g_1 is here directly but not exclusively to ancestral to g_2 because y, one the parents of a, does not belong to g_1.

Definition 3.3 *(Exclusively Ancestral Group)* Let there be g_1 and g_2 two monophyletic groups such that $g_1 \cap g_2 = \emptyset$, and a the unique included common ancestor of g_2. We can say that g_1 is an exclusively ancestral group of g_2 (or that g_1 is exclusively ancestral to g_2) if and only if for every $x \in X$, if $(x, a) \in p$ then $x \in g_1$.

In reality taxa can indeed be direct ancestors without being exclusive ancestors, as for example in the case of plants, which have two directly ancestral groups: protozoa and cyanobacteria (see for example Figure 7C).

Observation 3.4 *(Single Parenthood)* If the unique included common ancestor of g_2 does have only one parent (as for example in the case of a network without mergings) and if g_1 is directly ancestral to g_2, then we can trivially say that g_1 is exclusively ancestral to g_2.

Lemma 3.5 *(Transitivity)* Let there be three monophyletic groups g_1, g_2 and g_3. If g_1 is ancestral to g_2 and g_2 is ancestral to g_3 then g_1 is ancestral to g_3.

This lemma clearly echoes to Lemma 1.5, which demonstrates the transitivity of ancestrality between individuals.

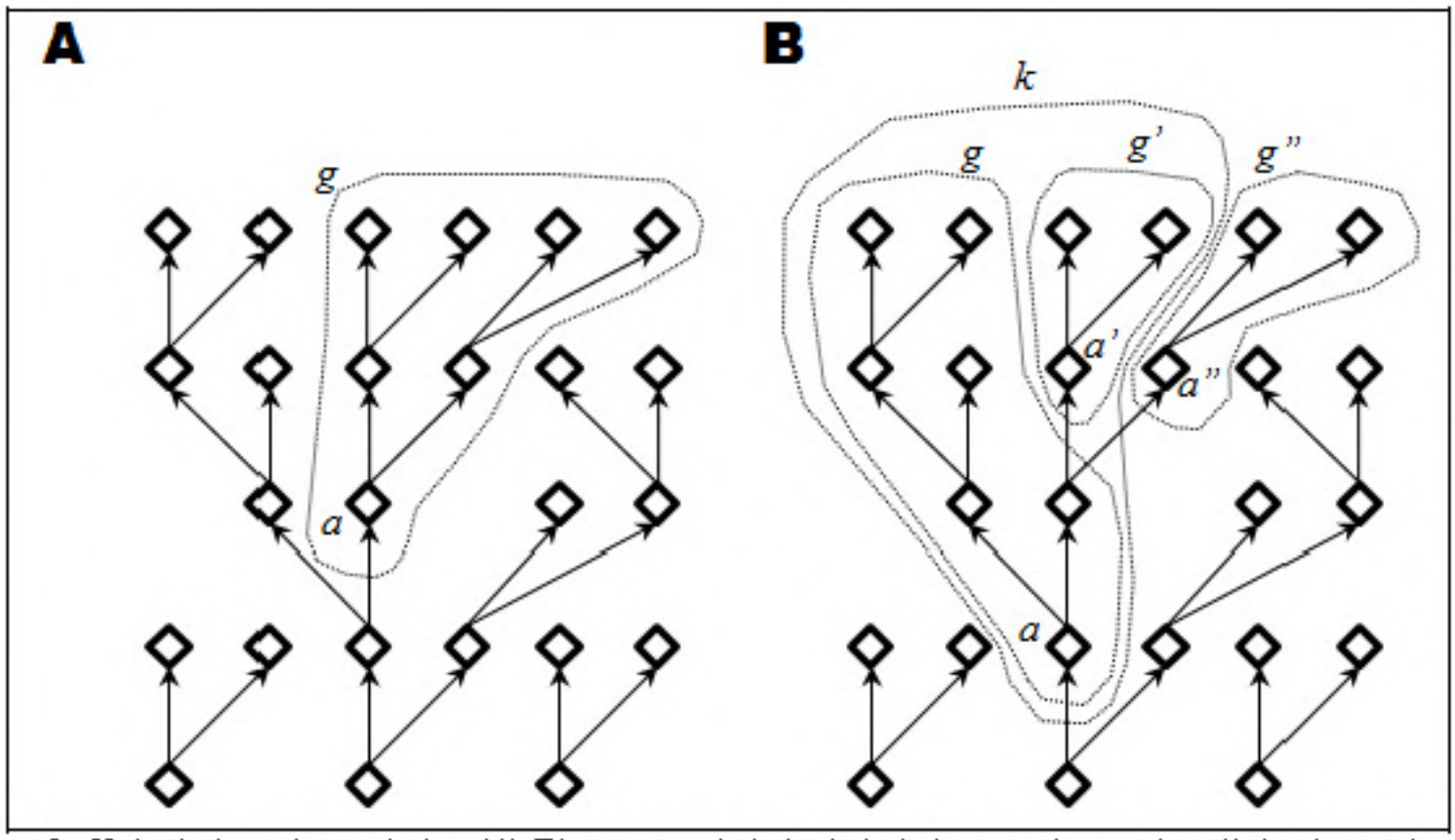

Figure 8. Holophyly and paraphyly. (A) The group g is holophyletic because it contains all the descendants of a, the included common ancestor of g. (B) The group g is paraphyletic because it does not contain all the descendants of a: a' and a'' for example. It is however monophyletic since it contains a, an ancestor of all the members of g. The group g', also monophyletic, is a group to which g is ancestral because a is an ancestor of a'. Thus by Theorem 3.6, the union k is a monophyletic group (here continuous).

Theorem 3.6 *(Monophyletic Union)* Let there be g_1 and g_2 two monophyletic groups such that $g_1 \cap g_2 = \emptyset$. The group $g = g_1 \cup g_2$ is monophyletic if and only if the group g_1 is ancestral to g_2 or else if g_2 is ancestral to g_1.

Theorem 3.7 *(Continuous Union)* Let there be g_1 and g_2 two continuous groups of G such that $g_1 \cap g_2 = \emptyset$. The group $g = g_1 \cup g_2$ is continuous if and only if the group g_1 is directly ancestral to g_2 or else if g_2 is directly ancestral to g_1.

By combination of Theorem 3.6 and Theorem 3.7, it is clear that the union of two distinct continuous groups but indirectly ancestral is a discontinuous group. Figure 8B depicts a union between two continuous groups.

4. CONCEPTS DERIVED FROM MONOPHYLY

Having firmly established the necessary foundations for our study, we can now define some derived concepts and explore their properties. The concept of paraphyly in particular is not really an issue since all authors do agree that to make one it is sufficient to remove some descendants of the cenancestor of a monophyletic group (Hennig 1966; Cavalier-Smith 1998; Mayr & Bock 2002; Barton et al. 2007).

Definition 4.1 *(Paraphyletic Group)* Let there be a group g, g is said to be paraphyletic if and only if g is monophyletic and there exists a pair $(x, y) \in p$ such that $x \in g$ and $y \notin g$.

Definition 4.2 *(Holophyletic Group)* Let there be a group g, g is said to be holophyletic if and only if g is monophyletic and there does not exist a pair $(x, y) \in p$ such that $x \in g$ and $y \notin g$.

Lemma 4.3 *(Monophyletic Alternative)* Let there be a monophyletic group g and a its cenancestor. The group g is paraphyletic if and only if there exists a certain $x \notin g$ such that a is an ancestor of x, otherwise g is holophyletic.

The topological difference between holophyly and paraphyly is depicted in Figure 8. Definition 4.1 and Definition 4.2 define these notions by referring to parenthood whereas Lemma 4.3 is a reformulation referring to ancestry. We saw in the Section 3 of this paper that there exists an historical argument in favour of rejecting the Hennigian definition of monophyly. Here we can see that this Hennigian concept can be expressed by another word: "holophyly", coined by Ashlock in order to resolve this absurd terminological controversy (Ashlock 1971; Ashlock 1972; Mayr 1974; Ashlock 1979; Mayr & Bock 2002). Surprisingly this new term, which is nevertheless logically independent of the philosophical debate between evolutionism and cladism, was firmly rejected by proponents of cladism (Nelson 1971; Nelson 1973; Hennig 1975). This lack of agreement on vocabulary had inevitably led to confusion and focused much of the discussion on the form rather than the content of the problem. It was impossible for evolutionists to abandon this word to cladists since they had no other term to account for their concept of monophyly, which combines both holophyly and paraphyly.

This is what I call the utilitarian argument: cladists can perfectly express their ideas by using "holophyly" instead of "monophyly", whereas evolutionists cannot assert their point of view without a word meaning "holophyly + paraphyly". Furthermore, such a concept is today generically useful in studies of unrooted phylogenetic trees where precisely it is *de facto* impossible to distinguish holophyly and paraphyly. This has even led to the (redundant) coinage of the new term "clan" so as to fill this gap (Wilkinson et al. 2007). Let us finally notice in support of this argument that the word "holophyly" is built from the root ὅλος "all", which makes the term both transparent and unequivocal. We will see later (see Section 5) a third and last reason to prefer our definition of monophyly.

Definition 4.4 *(Polyphyletic Group)* Let there be a group g, g is said to be polyphyletic if and only if there does not exist $a \in g$ such that a is a common ancestor of g.

Clearly, a polyphyletic group is by definition the contrary of a monophyletic group. Groups are always either monophyletic or polyphyletic, which is indeed an expected property (see Table 1).

<table>
<tr><td rowspan="2">Monophyletic</td><td>Continuous</td><td colspan="2">Holophyletic</td></tr>
<tr><td>Discontinuous</td><td>Paraphyletic</td><td rowspan="2">Heterophyletic</td></tr>
<tr><td colspan="3">Polyphyletic</td></tr>
</table>

Table 1. Logical links between phyletic relationships. A group is always either monophyletic or polyphyletic. A monophyletic group is either continuous or discontinuous. A holophyletic group is necessarily continuous whereas a paraphyletic group can be either. Finally, a heterophyletic group is either paraphyletic or polyphyletic.

Definition 4.5 *(Heterophyletic Group)* Let there be a group g and A the set of all the most recent common ancestors (cenancestors) of g, g is said to be heterophyletic if and only if for every $a \in A$, it exists $x \notin g$ such that a is an ancestor of x. If $A = \emptyset$ then g is also heterophyletic (and polyphyletic in this case).

A heterophyletic group is thus a group which does not comprise all the descendants of each and every of its cenancestors. The case $A = \emptyset$ does not concern biology much since it has long been demonstrated beyond all reasonable doubt that all extant organisms and fossils are descended from a last universal common ancestor (LUCA). This very particular case of polyphyly is mentioned only in discussions about the origin of life on Earth (since the concept of LUCA must not be confused with the very first organism) or elsewhere. The term "heterophyly" was coined only recently (Zander 2009) and its use is consequently still not very widespread despite its usefulness.

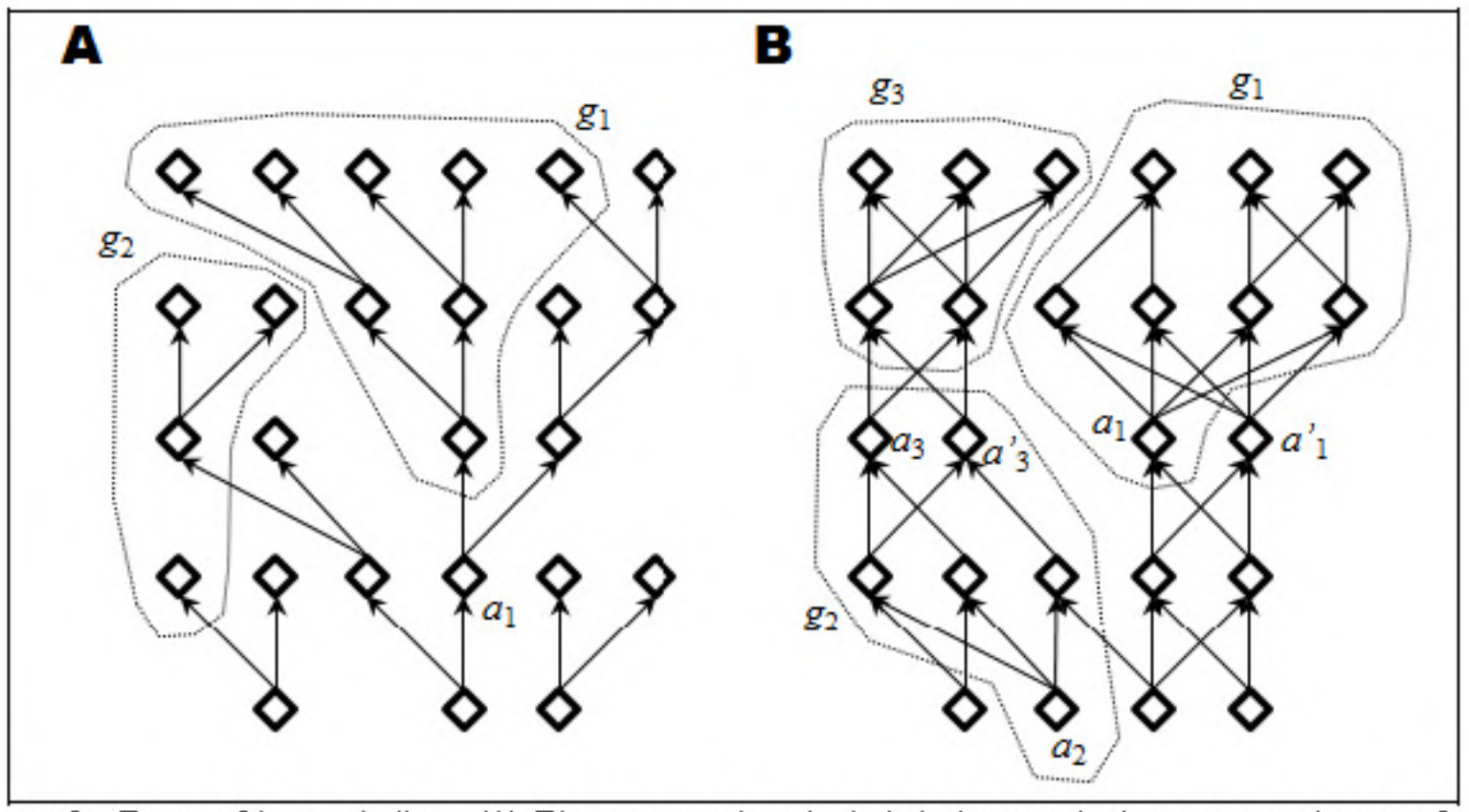

Figure 9. Types of heterophylies. (A) The group g_1 is polyphyletic because it does not contain any of the common ancestors of its members, for example a_1; the g_2 is polyphyletic because there does not even exist a common ancestor of all its members. (B) The group g_1 is not heterophyletic but holophyletic because it includes all the descendants of its cenancestor, here a_1. The group g_2 is heterophyletic because it does not include all the descendants of its cenancestor a_2; although it may seem counter-intuitive the group g_3 is also heterophyletic since it does not include any of its most recent common ancestors, a_3 or a'_3.

Lemma 4.6 Let there be a group g and $A \neq \emptyset$ the set of all the most recent common ancestors of g, g is heterophyletic if and only if g is paraphyletic or else if g is polyphyletic.

Observation 4.7 Let there be a group g and $A \neq \emptyset$ the set of the most recent common ancestors of g, g is heterophyletic if and only if g is not holophyletic.

This observation ensues from the fact that all groups are either polyphyletic or monophyletic and that all monophyletic groups are either paraphyletic or holophyletic (see Table 1). Heterophyly is depicted in Figure 9 in the context of a network with or without mergings. The main types of groups commonly encountered in scientific literature having been defined, the next parts of this paper shall consist in showing how it is possible to build a consistent Linnaean classification from this base material.

5. PARTITIONING THE DIFFERENT TYPES OF GROUPS

Taxonomy involves classifying the different organisms in disjoint sets, and the union of these sets must contain all the organisms. The use of set partitions in order to establish a model for classification of life seems therefore natural. In addition, we must join the condition of monophyly defined above.

Definition 5.1 *(Continuous Partition)* Let there be a group g, a continuous partition of g is a set $K = \{g_1, g_2, \ldots, g_n\}$ such that: firstly for every i, $1 \leq i \leq n$, $g_i \neq \emptyset$ and g_i is continuous; secondly if $n \geq 2$ then for every i, j, $1 \leq i < j \leq n$, $g_i \cap g_j = \emptyset$; and thirdly $\bigcup_{1 \leq i \leq n} g_i = g$.

A continuous partition is depicted in Figure 10.

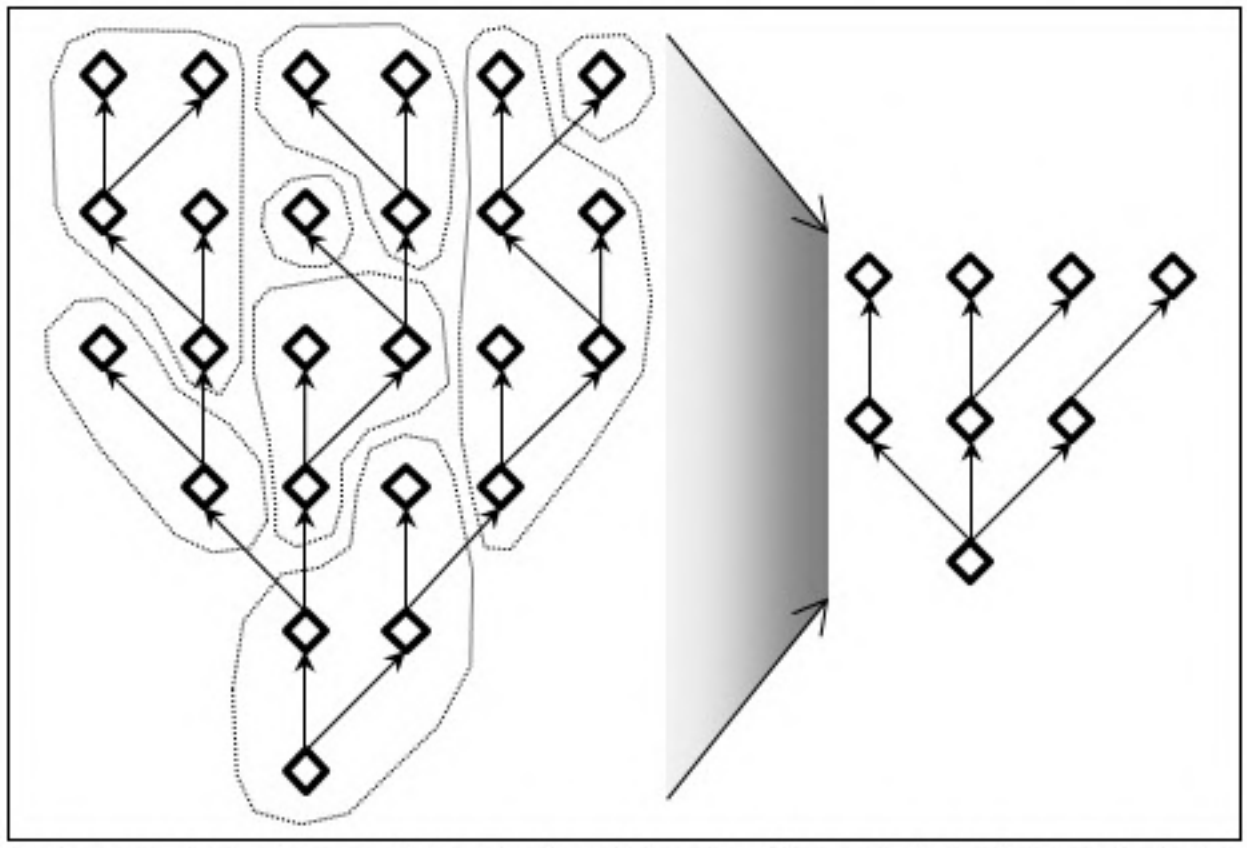

Figure 10. From a genealogical network to a phylogenetic one. The genealogical network depicted on the left is partitioned into continuous monophyletic groups (dotted lines). The relationships between individuals are thus replaced with relationships between directly ancestral groups. These groups and these relations can be depicted by a phylogenetic network (on the right) which is in fact the same mathematical object as a genealogical network (see Theorem 6.2).

Lemma 5.2 *(Existence)* It is always possible to define a continuous partition of a non-empty group. Such a partition can't have more parts than the whole group.

This means that in the limiting case every organism is just its own group. Indeed, the trivial set of all singletons is a continuous partition.

Observation 5.3 Let there be a continuous group g, the set $\{g\}$ is a trivial continuous partition of g.

Theorem 5.4 Let there be a continuous group g and $K = \{g_1, g_2, \ldots, g_n\}$ a continuous partition of g such that $n \geq 2$. It must then exist a certain i, $1 \leq i \leq n$, such that g_i is paraphyletic.

In whatever manner such a partitioning of a continuous group is handled, it is impossible to avoid the creation of paraphyletic groups. Kwok (2011) reached a very similar conclusion since he has shown that a consistent Linnaean classification though strictly holophyletic must contain only trivial monotypic groups ($n = 1$) except at the lowest rank (his Corollaries 43 to 45): we would thus have a unique species which comprises all organisms, then a unique genus composed of this sole species, then a unique family composed of this sole genus, etc. The condition $n \geq 2$ is therefore central to reveal that it is logically impossible to avoid paraphyly. This means that regardless of how it is taken, cutting branches of the tree of life automatically generates paraphyletic stems. This deduction, after all rather obvious, has been repeatedly reported (Meacham & Duncan 1987; Brummitt & Sosef 1998; Brummitt 2002; Brummitt 2003). For example Cavalier-Smith (1998) showed in the second figure of his paper that rejecting paraphyly involves not to classify some organisms. As he already stated in a previous paper:

"*It is impossible to cut up a phylogenetic tree into purely holophyletic groups: every cut generating a holophyletic branch necessarily also generates a paraphyletic stem.*" (Cavalier-Smith 1993)

This naturally led him to conclude that:

"*The dogma against paraphyletic taxa is logically incompatible with the acceptance of both evolution by descent and the goal of taxonomy as the creation of a comprehensive phylogenetic* classification of all organisms*, both extant and extinct.*" [my emphasis] (Cavalier-Smith 1998)

Not to classify all organisms at all levels is to say that for example some might be part of a family, but not part of a genus or a species, which is unacceptable. Although he stressed that his conclusion was correct, Kwok unfortunately did not drawn all the consequences from it by rejecting the principle of a purely holophyletic classification. Continuous partitions remain however a powerful tools to study the properties of different types of groups as we shall see in the rest of this paper.

Definition 5.5 *(Degree of Polyphyly)* Let there be a group g and $K = \{g_1, g_2, \ldots, g_n\}$ a continuous partition of g of cardinal n. We can say that n is the degree of polyphyly of g if there does not exist a continuous partition of g of cardinal inferior to n.

Observation 5.6 All continuous groups have a degree of polyphyly of 1.

This observation clearly derives from Observation 5.3. This leads us to notice how much the traditional definitions of monophyly (from ancient Greek μόνος "sole") and polyphyly (from πολύς "many") are consistent with the etymologies of these words. By removing paraphyletic groups from the concept of monophyly, Hennig's expropriation consequently removes certain groups which have nonetheless a degree of polyphyly of just one! Furthermore, the Definition 5.5 shows that a

polyphyletic group can easily be cut into several monophyletic groups (See Lemma 5.2). Thus, a *poly*phyly corresponds well and truly to a concatenation of several *mono*phylies, and not necessarily several *holo*phylies. This is what I name the morphosemantic argument: it is desirable for obvious logical reasons that the morphologies of these words are congruent with their semantical relationships.

In his paper Kwok (2011) also discusses these etymologies and claims he has demonstrated that a polyphyletic group is indeed the plural of a "monophyletic" (i.e. holophyletic) group. His definitions of "monophyly" and polyphyly are regrettably distorted, and his conclusion is consequently invalid. Firstly, as previously shown, his definition of "monophyly" does not require the inclusion of a common ancestor and hence doesn't properly capture this concept. Thus, many so-called "monophyletic" groups are in fact frankly polyphyletic (see Section 2 and Figure 6). Secondly, his definition of polyphyly is curiously restricted to the groups composed of *all* the descendants of their progenitors. Thus, a group like the one depicted in Figure 11A, which is patently polyphyletic for any systematician, would be considered as non-polyphyletic according to Kwok's definition! He logically concludes (his Theorem 22) that these very particular polyphyletic groups can be split into several "monophyletic" groups, which are in fact polyphyletic as well. It may be possible to see a confirmation bias in this kind of reasoning.

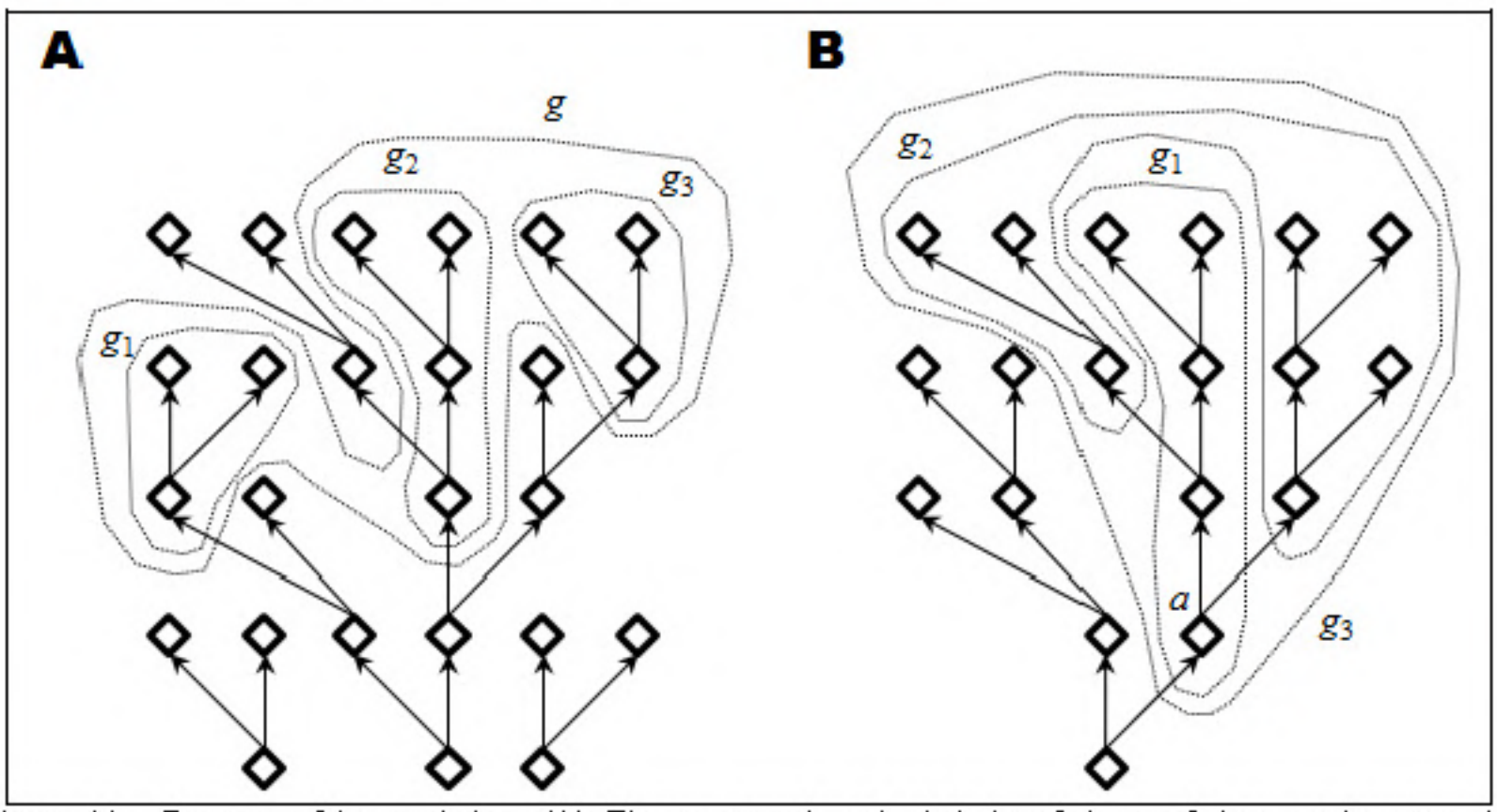

Figure 11. Degrees of heterophyly. (A) The group g is polyphyletic of degree 3 because it cannot be partitioned into less than 3 monophyletic groups, of which one is paraphyletic; this partitioning is unique. (B) The group g_1 is paraphyletic, g_3 represents the holophyletic group canonically associated to it and g_2 its complementary group; the group g_1 has a degree of paraphyly of 2 because the group g_2 has a degree of polyphyly of 2.

Theorem 5.7 *(Uniqueness)* Let there be g a group without mergings, polyphyletic of degree n, and $K = \{g_1, g_2, \ldots, g_n\}$ a continuous partition of g of cardinal n. Then, there does not exist any other continuous partition $K' \neq K$ of g such that $\mathrm{card}(K') = n$.

A polyphyletic group can therefore be uniquely split into a minimal number of monophyletic groups. They can be either holophyletic or paraphyletic (see Figure 11A). Of course, this theorem echoes the one of Kwok that we have just mentioned. By correcting the premises we come to a valid conclusion which reinforces our morphosemantic argument: a group arising from several origins can

be divided into several groups each of them arising from a unique origin. It is indeed in this spirit that Haeckel coined the opposition monophyletic/polyphyletic (see Section 2). Although formally independent, the morphosemantic argument and the historical one do strengthen each other.

The notion of paraphyly is often defined by opposition to holophyly (or "monophyly"). This definition is nearly always negative (some descendants are *removed*). We are nonetheless going to show that it is possible to expand the notion of paraphyly so as to make holophyly just a particular case of paraphyly.

Definition 5.8 *(Canonical Holophyletic Group)* Let a monophyletic group g et a the unique included common ancestor of g. Let us call g' the holophyletic group canonically associated to g if and only if for every $x \in X$, if a is an ancestor of x then $x \in g'$.

Definition 5.9 *(Complementary Group)* Let there be g a monophyletic group. We say that g' is the complementary group of g if and only if $g \cap g' = \emptyset$ and $g'' = g \cup g'$ is the holophyletic group canonically associated to g.

The canonical holophyletic group associated to a holophyletic group is always itself. Consequently, the complementary group of a holophyletic group is always the empty set.

Definition 5.10 *(Degree of Paraphyly)* Let there be g a monophyletic group and g' its complementary group. If g' is non-empty, then the degree of paraphyly of g is said to be the same as the degree of polyphyly of g'. If $g' = \emptyset$, the degree of paraphyly of g is logically 0.

The degree of paraphyly thus corresponds to the number of "branches", or clades, removed from the canonical holophyletic group (see Figure 11B). It is usual in scientific literature to find discussions about some taxa said to be "more or less" paraphyletic, or "more or less" polyphyletic. This "more or less" has sometimes been criticized because of the lack of a precise definition referring to such a vague notion of degree. All formal definitions of the base concepts I could find were limited simple dichotomies, sharply distinguishing holophyly from paraphyly and monophyly from polyphyly. Our study shows that it is possible to expand these notions by rigorously defining what degrees of polyphyly and paraphyly are. It is thus acceptable to define holophyly as being the property of a group having a degree of polyphyly of one and a degree of paraphyly of zero. This situation is comparable to modern physics where rest is regarded as a movement having a zero speed (as opposed to the archaic Aristotelian physics which sharply opposes rest and movement). There exists therefore a dialectal relation between monophyly and polyphyly, and also between holophyly and paraphyly (Envall 2008).

6. PHYLOGENY AND PHYLOGENETIC CLASSIFICATION

Our study has allowed us so far to form group and subgroups in our genealogical network. We have therefore finally all the necessary elements to make up a phylogenetic network as well as a phylogenetic classification.

Definition 6.1 *(Phylogenetic Network)* Let there be a genealogical network $G = (X, p)$. Let there be also X' a continuous partition of X, and p' a relation defined on X' such that $(g_1, g_2) \in p'$ for every $g_1, g_2 \in X'$, if and only if g_1 is directly ancestral to g_2. Then, the pair $G' = (X', p')$ is called a phylogenetic network.

Theorem 6.2 *(Sameness)* Every phylogenetic network is a genealogical network.

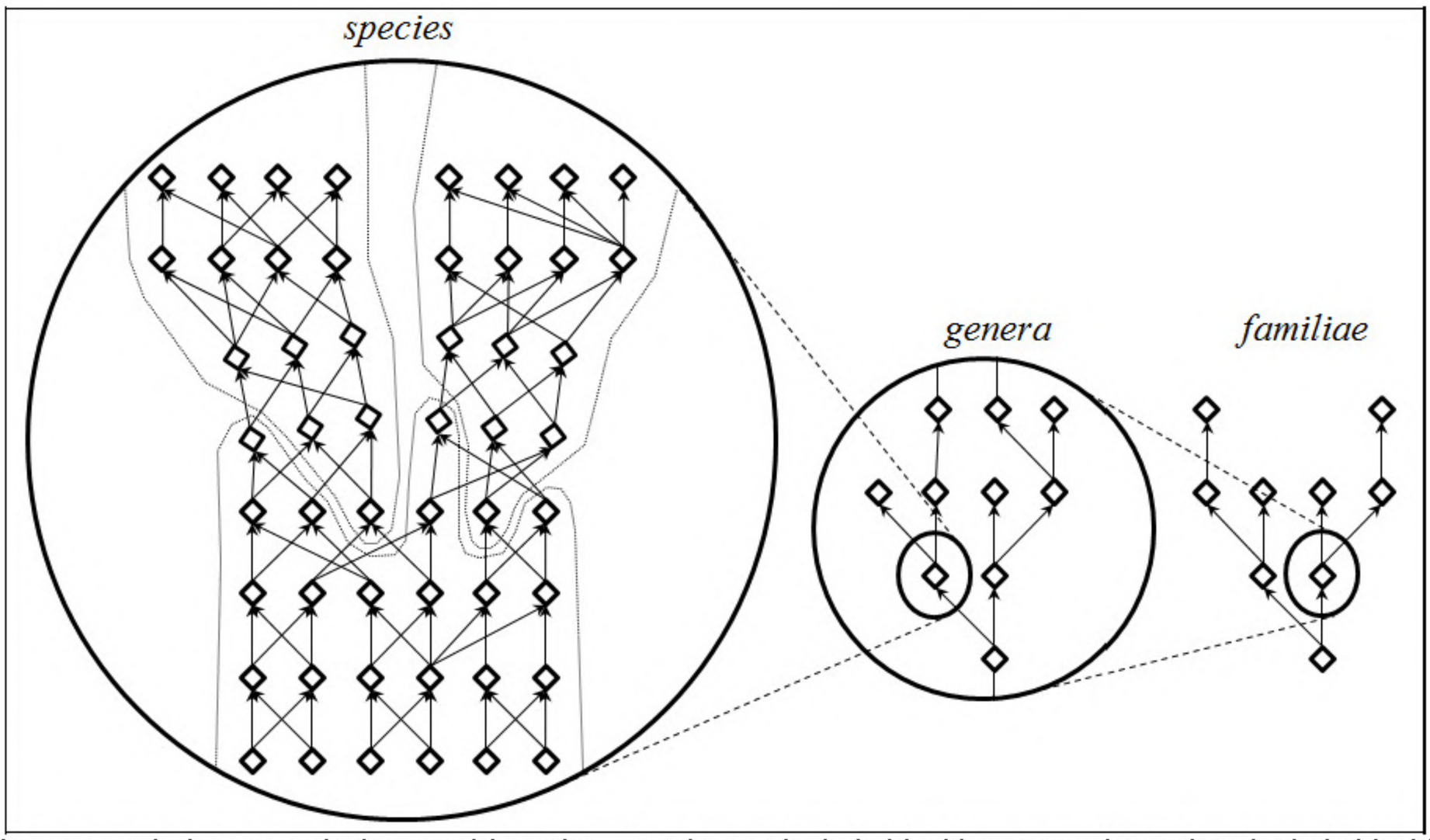

Figure 12. Phylogeny and Linnaean hierarchy. Species are included inside genera, themselves included inside families, etc.

We can deduce from this theorem that all the properties studied in genealogical networks on the scale of the relationships between individuals are also valid in phylogenetic networks on the scale of the relationships between groups (see Figure 10). This theorem is of crucial importance to the debate concerning the nature of phylogenetic trees: do their structures reflect real genealogies or else an abstract kinship? Our analysis clearly allows us to take a position in favour of the first option.

Definition 6.3 *(Linnaean Hierarchy)* Let there be a genealogical (or phylogenetic) network $G = (X, p)$. A Linnaean hierarchy is a sequence $X_1, X_2, \ldots, X_n$ such that $n \geq 2$, $X_1 = \{X\}$, and for every i, $1 \leq i \leq n - 1$, X_{i+1} is the union of fixed continuous partitions of the elements of X_i. For every i, $1 \leq i \leq n$, X_i is called a taxonomic category, whereas the elements of X_i are called taxa, and finally i is the rank of these taxa.

Our definition allows us to clarify the difference between a "taxonomic category" and a "taxonomic rank", which are often confused in practice. For example Animalia is a taxon that *has* the rank of kingdom (i = "*regnum*"), but we must say that it *belongs to* the category of kingdoms (Animalia $\in X_{\text{"regnum"}}$). Thus, a category is simply a set of all the taxa that have the same rank. In practice, X is the set of all organisms and X_1 is a set containing only one taxon which contains itself all organisms. For example if $X = \{a, b, c, d, e, f\}$ then $X_1 = \{\{a, b, c, d, e, f\}\}$. A continuous partition of the unique element of X_1 may be $\{\{a, b, c\}, \{d, e, f\}\}$, therefore $X_2 = \{\{a, b, c\}, \{d, e, f\}\}$. This set contains two elements, a continuous partition of the first one may be $\{\{a, b\}, \{c\}\}$ and a continuous partition of the second one may be $\{\{d\}, \{e, f\}\}$, therefore $X_3 = \{\{a, b\}, \{c\}, \{d\}, \{e, f\}\}$, and so on. The set $\{a, b, c\}$ of X_2 may be regarded as a kingdom, while the set $\{a, b\}$ of X_3 may be regarded as a phylum (see Figure 12).

Definition 6.4 *(Taxonomic Position)* Let there be a network $G = (X, p)$ and $X_1, X_2, \ldots, X_n$ a Linnaean hierarchy on this network. The taxonomic position of a taxon t_k of rank k is a sequence $t_1, t_2, \ldots, t_k$ such that $t_1 \in X_1$ and for every i, $1 \leq i \leq k - 1$, $t_{i+1} \in X_{i+1}$ and $t_{i+1} \subset t_i$. The taxonomic position of an individual is given by the smallest taxon to which it belongs, i.e. a taxon of rank n.

The taxonomic position indicates the location of a taxon in a Linnaean hierarchy. For example, the taxonomic position of the organism *a* is the sequence {*a*, *b*, *c*, *d*, *e*, *f*}, {*a*, *b*, *c*}, {*a*, *b*}, etc. As indicated in the definition above, such a classification is inclusive, i.e. made of *nested* groups. These groups are however not *embedded*: a taxon is composed of organisms, not of taxa of lower rank. Thus, we should not say that the genus *Caenorhabditis* belongs to the family Rhabditidae, but rather that it is included in it.

This classification is based on no other formal criterion that the respect of continuous monophyly. Other criteria needed to validate a given taxon are exclusively of biological nature and therefore rely on evolutionary, ecological and phenetic considerations to decide between different possible formal divisions. The name of "evolutionary classification" is thus plainly justified. As a consequence of Lemma 5.2, which specifies that a division into monophyletic groups is always possible, all individuals of a genealogical network do have a taxonomic position regardless of the complexity of the network (see Figure 12). A phylogenetic classification (in an evolutionary sense) is therefore a consistent classification scheme.

7. NOTION OF CLADE

Maybe we could blame our definitions of phyletic relationships for their lack of operationality because they refer to unknown ancestors (Nelson 1973). It is true that the labour of phylogeneticists is precisely to reconstruct the relationships of the species they study from very fragmented data. Thus the construction of a phylogenetic tree often requires going through the elaboration of a cladogram, a type of diagram depicting the genealogical relative proximity (or degree of kinship) of different sampled species. Yet it just so happens that some authors have proposed definitions of "monophyly" only by referring to topological relationships that connect the species studied in such a diagram:

"*Monophyly: a quality of a group including all species, or groups of species, assumed to be descendants of a hypothetical ancestral species.* […]" (Nelson 1971)

In this definition the most recent common ancestor (cenancestor) is explicitly excluded. When we defined monophyly and associated concepts in previous sections our goal was to represent a certain reality, whether it is accessible or not to us. Here our goal is to represent our knowledge of a certain reality. We must not confuse reality and the knowledge we have of it, that's why we have to use another term that "monophyly" to depict it.

Definition 7.1 *(Holoclady)* Let there be a genealogical or phylogenetic network $G = (X, p)$, a non-empty subset $K \subset X$ and A the set of all the common ancestors of a certain group $g \subset K$. The group g is said to be holocladic if and only if $A \neq \emptyset$ and there exists an $a \in A$ such that for every $x \in K$, if $x \notin g$ then a is not an ancestor of x. Such a common ancestor is called an exclusive common ancestor of g in K.

In the definition above, K may represent the set of all "accessible" organisms: for example all extant organisms, or else all known organisms (eventually from palaeontology), or else simply all the organisms included in a given study. The group g represents the sample under focus (see Figure 13A). A holocladic group is often simply called a "clade". The concept of clade initially referred to any monophyletic group *sensu* Haeckel (Huxley 1959), but the redefinition made by Hennig, however in the ambiguous sense of "holophyly or holoclady," is now universally accepted (Cavalier-Smith 2010a).

Having shown that genealogical and phylogenetic networks are the same, in the definition above X could be either a set of organisms or else a set of groups of organisms, in the same way as the

elements x could be either organisms or else groups of organisms. An exclusive common ancestor is not necessarily unique, as it is the case for example in sexual reproduction. All the most recent common ancestors need not to be exclusive in order for a group to be holocladic (see Figure 13B). By the way, an exclusive common ancestor is not always a most recent common ancestor (see Figure 13C). Just as we previously defined an opposite term to each phyletic relationship (see Table 1), the definition of the opposite notion of a clade is designed in order to simplify wording in systematics' discussions.

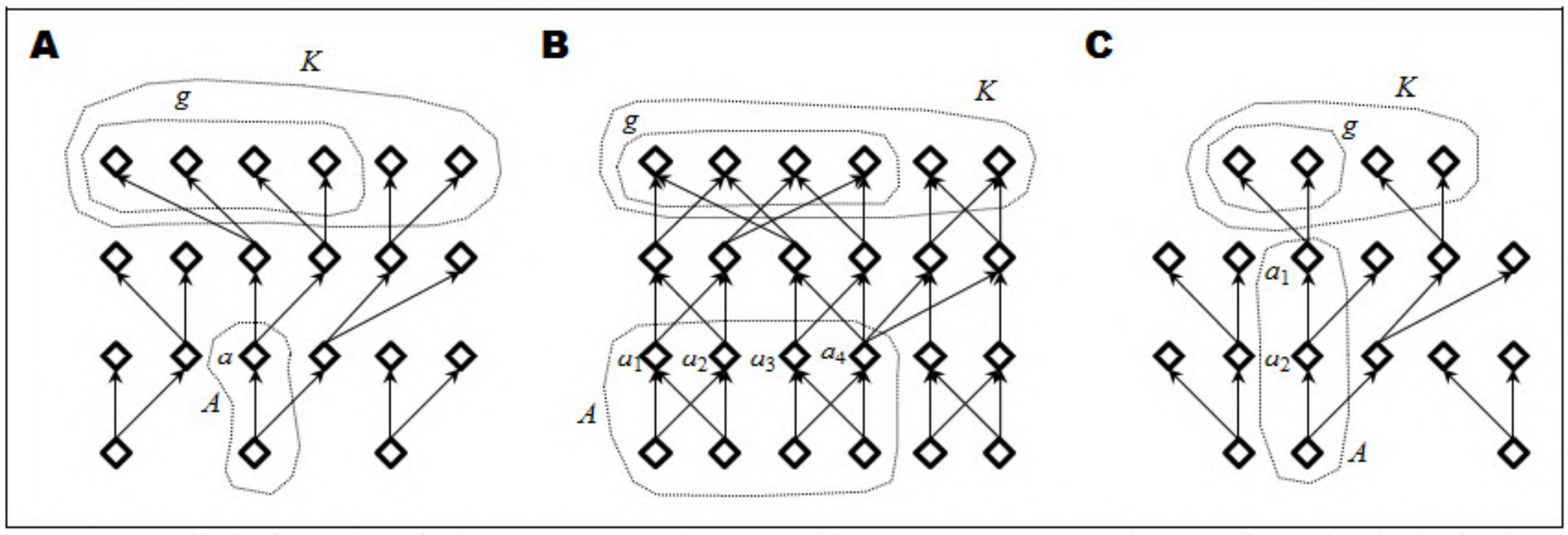

Figure 13. Holoclady and exclusive common ancestors. The set K represents the set of species included in the study, g is a group that we want to validate as a clade, A is the set of the common ancestors of g. (A) Example of a holocladic group in a network without mergings, a is both a most recent common ancestor and an exclusive common ancestor of g in K. (B) In this network with mergings, a_1, a_2 and a_3 are exclusive common ancestors of g but this is not the case for a_4 because, although it is also a most recent common ancestor of g, some of its descendants in K do not belong to g. (C) In this example a_1 and a_2 are both exclusive common ancestors of g in K but only a_1 is a most recent common ancestor of it.

Definition 7.2 *(Heteroclady)* Let there be a genealogical or phylogenetic network $G = (X, p)$, a non-empty subset $K \subset X$ and A the set of all common ancestors of a certain group $g \subset K$. The group g is said to be heterocladic if and only if $A \neq \emptyset$ or if for every $a \in A$ it exists a certain $x \in K$ such that a is an ancestor of x and $x \notin g$.

Observation 7.3 *(Potential Polyphyly)* Let there be g a holocladic or heterocladic group and A the set of all its common ancestors. The group g is polyphyletic if and only if $A \cap g = \emptyset$, otherwise it is monophyletic.

This observation comes directly from Definition 2.3 and Definition 4.4, and is clearly depicted in the three examples of Figure 13. This result seems to contradict intuition because of the very frequent confusion between the concepts of holoclady and holophyly. This confusion comes from the misleading terminology of cladists that use the same word "monophyly" to refer to both concepts. Let us notice also that the ancestors are not necessarily excluded from the studied group, since it is *a priori* impossible to know that no species is an ancestor of another one in the studied sample.

Definition 7.4 *(Canonical Holophyletic Group)* Let there be g a holocladic group defined in K on the network $G = (X, p)$, A the set of all the common ancestors of g and $a \in A$ an exclusive common ancestor of g. We call a canonical holophyletic group of g any holophyletic group g' such that a is the unique included common ancestor of g'.

Because there can be several exclusive common ancestor, there may also be several canonical holophyletic groups. This definition recalls us how much holoclady and holophyly are distinct

concepts. Although sometimes a holocladic group is itself its own holophyletic group canonically associated, the word "clade" should not be used as a synonym for "holophyletic group" because if may unnecessarily increase the confusion between holoclady and holophyly.

Lemma 7.5 If g' is a canonical holophyletic group of a clade g, then $g \subset g'$.

Definition 7.6 *(Degree of Heteroclady and Canonical Holocladic Group)* Let there be g a heterocladic group. Let there be $n \geq 1$, then it is said that the degree of heteroclady of g is inferior or equal to n if and only if it exists n holocladic groups g_i such that $g' = g \cup \bigcup_{1 \leq i \leq n} g_i$ is a holocladic group under the condition that for every i, $1 \leq i \leq n$, for every j, $1 \leq j \leq n$, with $i \neq j$, then $g_i \cap g_j = \emptyset$ and $g_i \cap g = \emptyset$. These groups are called complementary groups of g, and g' is the holocladic group canonically associated to g.

Observation 7.7 Holoclady is naturally associated to a null degree of heteroclady: there is no complementary group and $g = g'$.

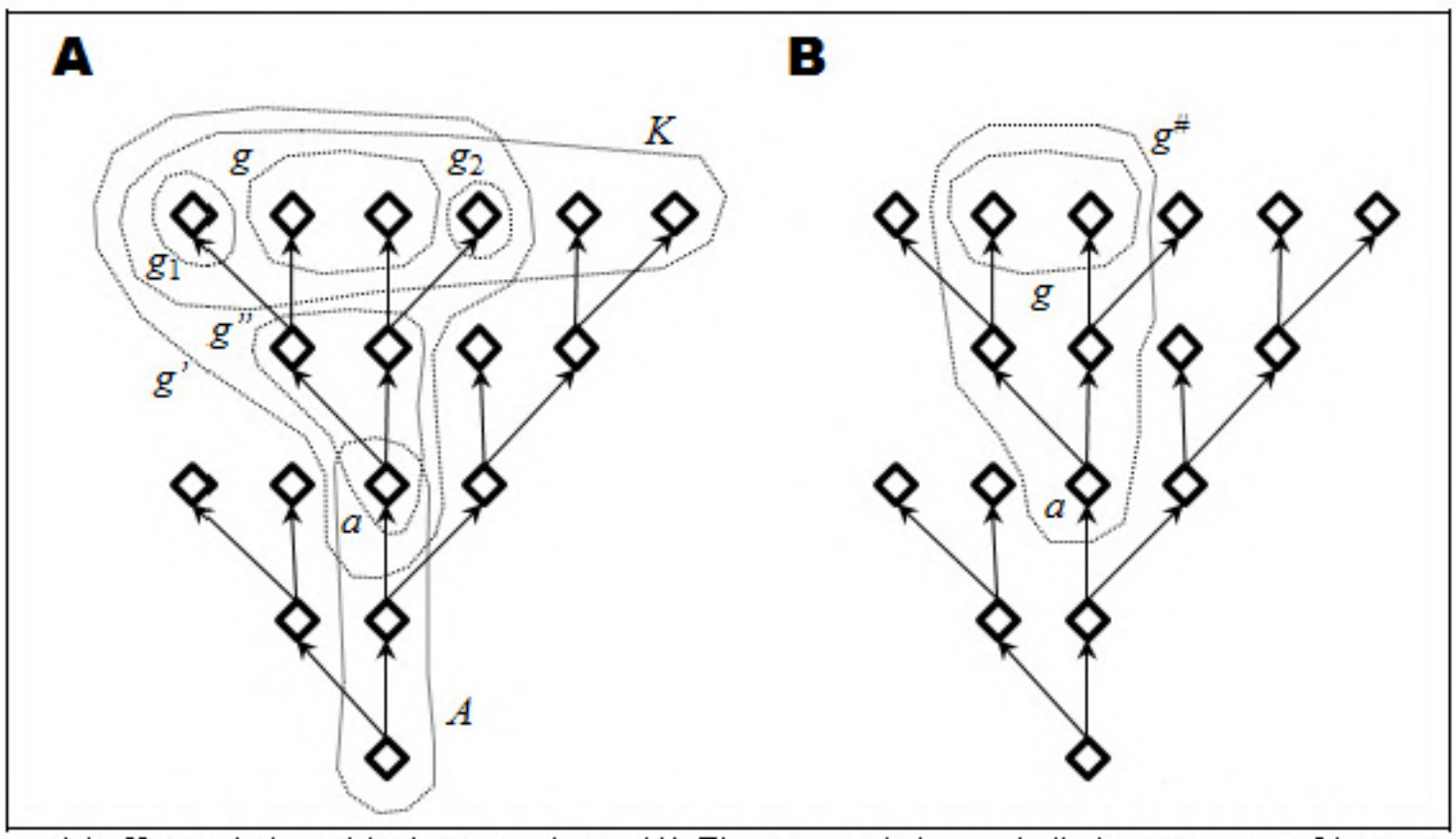

Figure 14. Heteroclady and its interpretations. (A) The group g is heterocladic because none of its common ancestors depicted by the set A is an exclusive common ancestor of its elements in the subset K. The groups g_1 and g_2 are the complementary groups of g in K because the union $g \cup g_1 \cup g_2$ is holocladic, the degree of heteroclady of g is therefore 2. The sole exclusive common ancestor of its associated holocladic group is a, which leads to the definition of g', constituted of a and all of its descendants, as the holophyletic group canonically associated to g. The group g'', constituted solely by the elements of g' absent from K, is the basal group of g. (B) The group g can be interpreted as being simply an invalid polyphyletic group or else as revealing the existence of a natural group $g^{\#}$, paraphyletic of degree 2.

A heterocladic group has no exclusive common ancestor, but it is however possible to attribute to this group a canonical holophyletic group by associating to it the one of its own canonical clade (see Figure 14A). This means that a holocladic pattern suggest the existence of a real situation of holophyly, whereas a heterocladic pattern only indicates a lack of holophyly: it is not then possible to formally decide between a real situation of paraphyly or of polyphyly (see Figure 14B). Biological arguments are thus necessary to determine if it is relevant or not to include a cenancestor of the group

in it. It is a complex decision which largely depends on our knowledge on ecology, evolutionary mechanisms, palaeontological data, etc.

This may explain in part the attractivity of an automatical method which, by rejecting any heteroclady and therefore putatively any heterophyly, covers up these difficult dilemmas in the labour of phylogeneticists, but without really resolving them… This led to the reinforcement of two opposing attitudes, equally disastrous for both stability and relevance of the classification of life. Firstly, *lumping* consists in always unifying heterocladic groups with their complementary groups, which consequently drowns homogeneous and relevant taxa inside too large and too heterogeneous groups. Secondly, *splitting* consists on the contrary in dividing heterocladic taxa in smaller holocladic groups, which consequently leads to the disjunction of similar sets. This could have led for example to an explosion of the number of "phyla" or on the contrary to the merging of many genera thus containing very different species.

To describe similar concepts to those of holoclady and heteroclady, Podani respectively coined the terms "monoclady" and "paraclady" (Podani 2009; Podani 2010a; Podani 2010b; Podani 2013). In the context of synchronic classification, i.e. a precise slice of time, he states that "a group is monocladistic if it includes all terminals of a given clade" (Podani 2009). As a consequence, a "monocladistic" pattern suggests the existence of a situation of holophyly and *a priori* excludes paraphyly (however we will see that this must be nuanced). Since "monoclady" implies the rejection of this type of monophyly, the replacement of this misleading term by "holoclady" seems rather wise. Moreover this modification seems to be in the spirit of Podani's coinage since he created his term by contrast to "monophyly" *sensu* Hennig, i.e. holophyly.

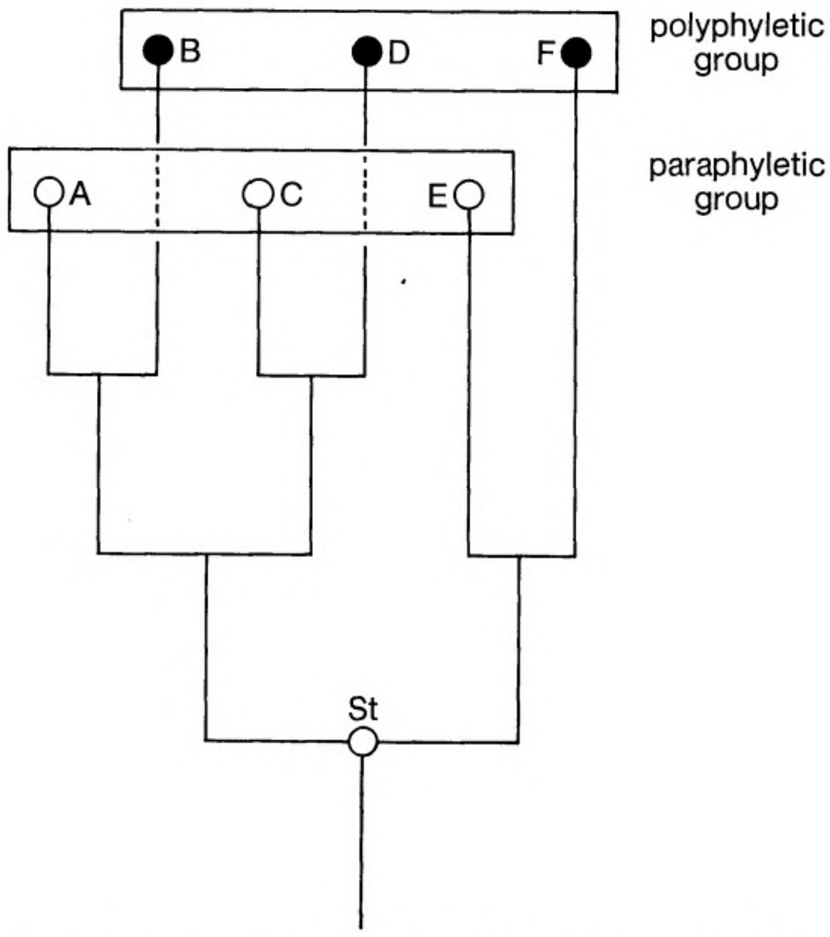

Figure 15. An impossible topological distinction: "polyclady" vs "paraclady". The white circles represent the primitive state of a character while black circles represent the derived state. Figure reproduced with permission from Hennig (1975).

Concerning "paraclady" Podani states himself: "Paraclady means that the group cannot be embedded into a monophyletic taxon [i.e. holophyletic], and it is therefore indication of paraphyly or even polyphyly in the corresponding diachronous classification" (Podani 2009). That is to say, "paraclady" corresponds to both types of heterophyly, and not only paraphyly (see Figure 14B). Symmetrically, the term of heteroclady seems to be more appropriate than the misleading term of

"paraclady". In order to build a complete set of analogous pairs Podani also coined the term "polyclady" (Podani 2010a). Logically, he could not succeed in distinguishing clearly between "paraclady" and "polyclady", and therefore made the later a subcase of the former. Hennig had already faced this problem and had to rely on biological considerations (primitive or derived state of a character) to distinguish these two topologically identical situations (see Figure 15). As noticed by Cavalier-Smith (2010a), the diagram drawn by Hennig do not depicts correctly an opposition between paraphyly and polyphyly since the common ancestor "St" is excluded from both groups. Nelson (1971) proposed to topologically distinguish "paraphyly" and "polyphyly" by defining the first term as a heteroclady with a degree of one and the second term as a heteroclady with a degree strictly superior to one. These definitions were never very successful among taxonomists who have always preferred to refer to the inclusion or exclusion of the common ancestor. It does not seem relevant to me to give different names to different degrees of the same kind of pattern.

Recently some cladists seem to have realized that it was not only necessary to distinguish between the notions of holophyly and holoclady but also to make them coexist by using different terms (Vanderlaan et al. 2013). To refer to them they coined respectively the words "diamonophyly" and "synmonophyly". Two of the coauthors, Williams and Ebach, were however aware of the terms coined by Podani since they blasted this conceptual distinction by commenting his paper (Podani 2009) in their blog[1]. The problem is not, quite the contrary, that they have changed their minds and have finally understood the relevance of this distinction. But beyond the derogatory tone, it is particularly sad that they did not bother to even mention Podani in their own article (Vanderlaan et al. 2013) and did not therefore recognize him the authorship of the idea to distinguish these two concepts by two different words.

The term of "monoclady" was moreover preferable to "synmonophyly" because it deletes the Haeckelian etymon *phylon* which designates the origin of a lineage (Dayrat 2003), yet it is precisely not a matter of origin when talking about holoclady. Furthermore, the use of the prefix "syn-" and "dia-" directly refers to the distinction between synchrony/diachrony, also made by Podani. This distinction is unfortunately very misleading! On the one hand, because some extant species are in fact ancestral to other extant species (see Section 10.2). On the other hand, a diachronic study (i.e. including fossils) can perfectly produce relevant cladograms showing holocladies. The metaphysical distinction between synchrony and diachrony is thus not relevant to taxonomy. One must keep in mind that the set K that is studied is plainly arbitrary and has no relation with the physical notion of time. Even if somehow the orientation of graphs reveals a chronological sequence, it must be understood that the time axis is absent from these representations, which explains that individuals and even taxa are represented by points and not by bars. Finally contrary to Podani, I recommend for the adjectival form to simply use the suffix "-ic" instead of "-istic". It is indeed desirable to distinguish cladic things, i.e. things related to clades or to their properties, from cladistic things, i.e. things related to the treatment of clades in general or to cladistics in particular.

Definition 7.8 *(Crown-Group and Basal Group)* Let there be g a clade defined in K on the network $G = (X, p)$, A the set of all the common ancestors of g, A' the set of all the exclusive common ancestors of g in K and g' a holophyletic group canonically associated to g such that its unique included common ancestor $a \in A'$ is a most recent common ancestor of g. Let us then define the group g'' such that for every $x \in X$, $x \in g''$ if and only if $x \in g'$ and $x \notin K$. The group g'' is called the basal group of the clade g relatively to g'. By opposition g is called the crown-group.

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[1] http://urhomology.blogspot.fr/2009/12/paraphyly-watch-4-monoclady-and.html; entitled "Paraphyly Watch 4: Monoclady and Paraclady" ; posted on Monday 7th December 2009 ; accessed on Monday 22th December 2014.

Observation 7.9 Let there be g a clade, g' canonical holophyletic group of g and g'' the basal group of g relatively to g', then it is always true that $g' = g \cup g''$ and $\emptyset = g \cap g''$.

Because the definition of a basal group depends on the canonical holophyletic group on which it is constructed, if this later one is not unique then the basal group is also not unique. In the same way we have expanded the definition of a canonical holophyletic group in the case of heterocladic groups, it is possible to expand to them the definition of basal groups by taking as an intermediary a canonical holocladic group. The crown-group would then be the initial heterocladic group itself (see Figure 17A).

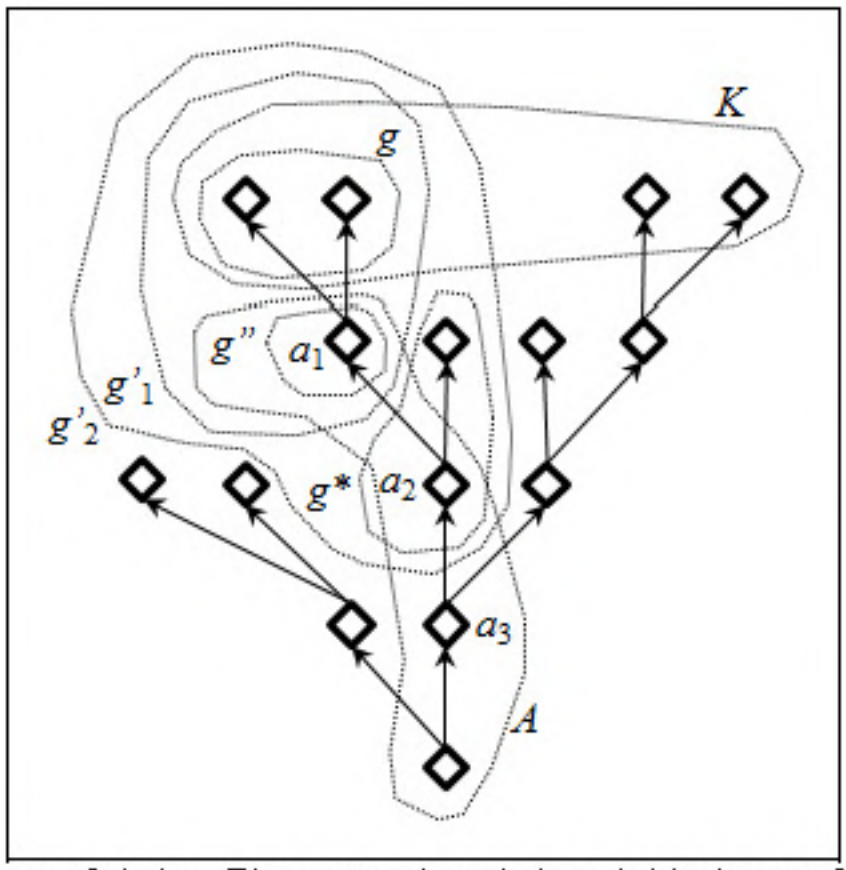

Figure 16. Accessory groups of clades. The group g is a clade and A is the set of all its common ancestors. Among them a_1 and a_2 are exclusive common ancestors in K. The individual a_1 is the most recent common ancestor, so it permits the definition of the smallest holophyletic group canonically associated to g, i.e. g'_1. The basal group g'' is therefore complementary to g in g'_1, here: $g'' = \{a_1\}$. On the contrary, g'_2 is the largest holophyletic group that be canonically associated to g, so it permits the definition of g^* the stem-group of g, the complementary group of g'_1 in g'_2.

Definition 7.10 *(Stem-Group)* Let there be g a clade defined in K on the network $G = (X, p)$, A the set of all the common ancestors of g, A' the set of all the exclusive common ancestors of g in K, A^* the set of all the most recent common ancestors of g, and $H = \{g'_1, g'_2, \ldots, g'_n\}$ the set of all holophyletic groups canonically associated to g. Let us consider one of these groups $g'_k \in H$ with k, $1 \leq k \leq n$, such that its unique included common ancestor $a_k \in A' \cap A^*$. Then we define a stem-group g^* such that for every $x \in X$, $x \in g^*$ if and only if $x \in \bigcup_{1 \leq i \leq n} g'_i$ and $x \notin g'_k$.

Lemma 7.11 *(Anteriority of Stem-Groups)* The unique included common ancestor of a non-empty monophyletic stem-group is never a most recent common ancestor of the clade from which it has been defined.

This lemma shows us that in accordance with intuition, stem-groups are necessarily "older" than basal groups, and *a fortiori* than crown-groups. Basal groups and stem-groups are both called the "accessory groups" of a clade (see Figure 16). The beginnings of these concepts were already present in Haeckel's work (Dayrat 2003).

Like basal groups, delineation of stem-groups depends on the most recent common ancestor that has been selected: if there are more than one, then there are several slightly different stem-groups. These concepts are especially relative since the delimitation of the subset K is itself arbitrary. So in practice, it is always needed to specify in what context a clade is studied before we can talk unambiguously about basal groups and stem-groups. The stem-group witnesses a series of evolutionary innovations that precede the most recent common ancestor of a clade, its study can therefore help to understand how the basal group and the crown-group successively emerged. To take a classical example, it would be very difficult to accurately explain the mechanisms that led to the emergence of the class Aves from the class Reptilia if we were neglecting the study of the stem-group of modern birds, which contains the extinct superorder Dinosauria plus the primitive birds.

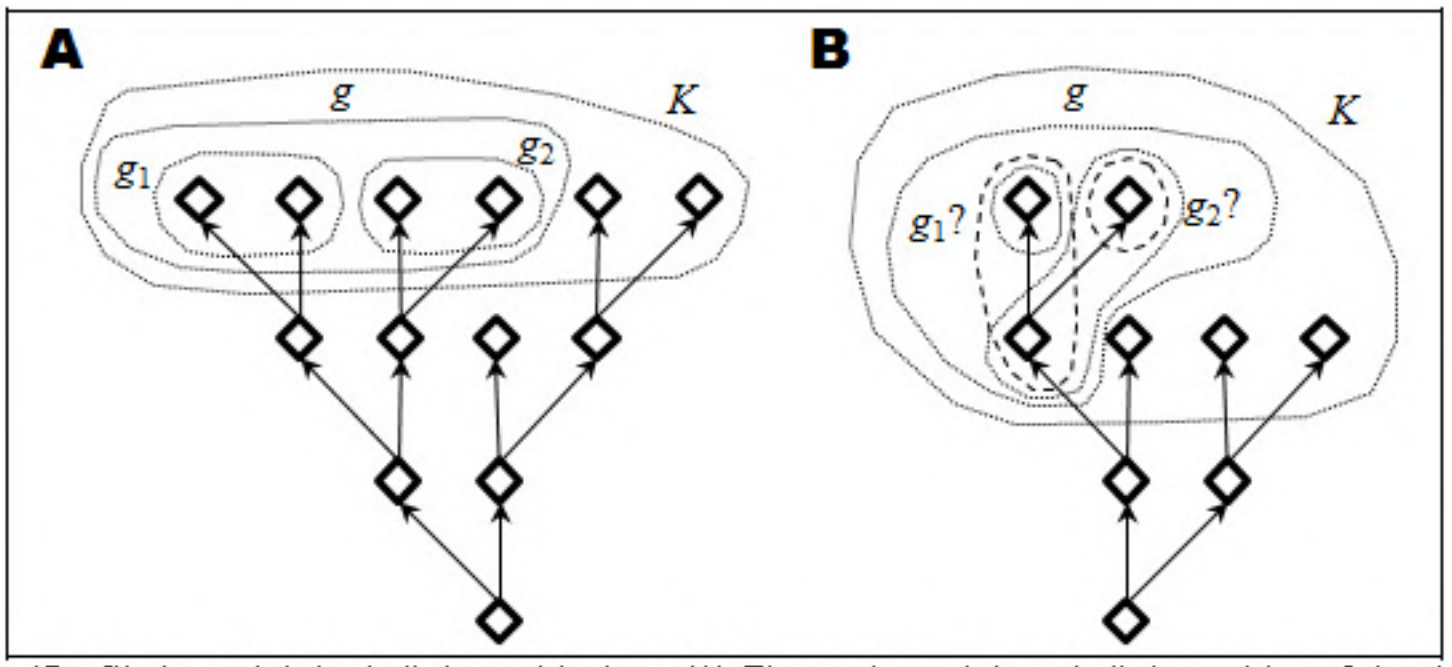

Figure 17. Clades and their cladistic partitioning. (A) The set $\{g_1, g_2\}$ is a cladistic partition of the clade g defined in K. (B) It is not possible to chop up the clade g into two non-overlapping clades, thus this clade have no cladistic partition.

Lemma 7.12 *(Paraphyly of Basal Groups)* Non-empty basal groups are necessarily paraphyletic.

This lemma is however not true concerning stem-groups since they result from the union of potentially several paraphyletic groups whose cenancestors are not necessarily ancestral to each other. A stem-group can thus be polyphyletic.

Lemma 7.13 *(Heterophyly of Stem-Groups)* Stem-groups can never be holophyletic.

The concepts of crown-group and stem-group have developed over the past fifteen years, spreading rapidly in the scientific literature. They do not conform to the current cladist paradigm that regards as useful only clades, as both units of the classification of life and as operational units in the phylogenetic studies. The success of these concepts in this theoretical context that is most unfavorable to them is indicative of the practical need to distinguish the notions of taxon, clade and grade. It is not difficult to assume that without an opportunity to express in a clear language the historical succession of different grades it was tough enough to intelligibly explain the emergence of different taxa through time, i.e. phylogenesis. Similarly, the explosion of the use of quotation marks systematically surrounding the words “reptile” or “fish” rather than the cladists’ desired complete disappearance of these terms says the refinement of a jargon superficially consistent with this paradigm but actually secretly calling for ideas that are contrary to it. In the same way, the spread of

surprising paraphrases such as "non-avian dinosaurs" reflects the unconscious and involuntary hypocrisy into which many colleagues are unfortunately forced.

Moreover, contrary to what one might naively believe the finding of a holoclady is not formally sufficient to conclude immediately that there exists a holophyly: "If a collection of organisms is found to be monocladistic [i.e. holocladic] (in a molecular study, for example), then the taxon which includes this group in a diachronous classification is not necessarily monophyletic [i.e. holophyletic]" (Podani 2009). Indeed, a clade arises from the same stem-group as its sister clade. This implies that stem-groups can either be classified as a taxon in its own right or be united with one of its daughter clades. A wise classification must therefore be based on a rigorous reconstruction of the ancestors in order to classify them.

Cavalier-Smith (2013) wonderfully illustrates how not to fall into such a trap concerning choanoflagellates, a group of paraphyletic protozoans which gave birth to the animal kingdom but whose extant members now form a holocladic crown-group:

"It is an illusion to claim that choanoflagellates are holophyletic and that one could make a holophyletic phylum restricted to them alone. Prior to the origin of epithelia and mesenchyme the lineage that later led to animals was beyond all reasonable doubt choanoflagellate in morphology and life style; because this lineage did not generate any surviving choanoflagellates, they were stem choanoflagellates not crown choanoflagellates. Crown choanoflagellates (defined as the last common ancestor of all extant choanoflagellates plus all its descendants) are indeed holophyletic. But crown choanoflagellates are a clade and should not constitute a taxon."

Let us take this opportunity to point out, as does Cavalier-Smith, how much it is simply impossible to avoid paraphyly in a comprehensive classification based on phylogenetic tree (see Section 5):

"To create an illusion of 'avoiding' paraphyly, equating Choanoflagellatea with crown choanoflagellates only, would leave stem choanoflagellates unclassified, equivalent to cutting up the phylogenetic tree into pieces, throwing away all the stems, and classifying only the terminal branches – yielding a phylogenetically misleading and fragmented picture of the tree of life. That is not a 'phylogenetic classification' as often claimed, but an incomplete and conceptually defective one."

To distinguish cases of obvious paraphyly suggested by heteroclady and cases of paraphyly hidden by holoclady, I suggest using the term "cryptic paraphyly." These cases should be reported in any good classification because they carry important historical information. Thus, a taxon known to be cryptically paraphyletic is also known to be directly ancestral to some other taxa even if its extant members do share an exclusive common ancestor.

8. CLADOGRAMS, CLADIFICATION AND CLADONOMY

Contrary to a Linnaean hierarchy, which uses taxa as classification units, the "classification" promoted by cladists uses clades. This ordering system is called a cladification so as to clearly differentiate it from a classification. Indeed, a classification can be defined as a "hierarchically ordered systems of classes of *similar* objects [my emphasis]" (Mayr & Bock 2002). The composition of clades may instead be very heterogeneous. It is therefore important to distinguish between an "arrangement" and a "classification", as well as between the verbs "to arrange" and "to classify" (see Table 2). This opposition between arrangement of clades and classification of taxa is also made by some cladists, although with different words (Griffiths 1974).

ACTIVITIES

To categorize: To put sets of objects into order. The result is a *categorization*. It is composed of categories, i.e. sets of sets.

To arrange: To put objects into order by assigning ranks to them or by distributing them into sets according to certain criteria. The result is an *arrangement*.

To classify: To distribute objects into distinct *classes*, i.e. sets whose members share a greater *affinity* with each other than with members of the other such sets. The result is a *classification*, a particular type of arrangement.

To group: To join distinct individuals together into larger and larger sets (upward strategy). The result is a *grouping*, a particular mode of arrangement or categorization.

To hierarchize: To assign ranks to sets of objects. The result is a *hierarchy*, a particular type of categorization analogous to rankings regarding arrangements.

To rank: To assign ranks to objects so as to order them into a certain sequence (alphabetical, chronological, etc.). The result is a *ranking*, a particular type of arrangement.

To sort: To successively divide a set of distinct individuals into smaller and smaller sets (downward strategy). The result is a *sorting*, a particular mode of arrangement or categorization.

DISCIPLINES

Cladonomy: Side activity of systematics which consists in allocating scientific names to clades. Cladists recognize these clades as natural groups and arrange them into a cladification, which is truly an arrangement but not a classification.

Phylogenetics: Discipline that aims at reconstructing the evolutionary history of the living world so as to explain its progression (i.e. phylogenesis) by making a synthetic structured representation of it (i.e. phylogeny). In practice, phylogenetics handles groups that have been identified by taxonomy and cladonomy.

Systematics: Scientific study of living organisms in their diversity and their evolutionary relationships. Systematics comprises two complementary facets: phylogenetics and taxonomy.

Taxonomy: Discipline whose field of research includes identification, description, recognition and classification of the organisms of the living world into groups called taxa. One of the main goal of taxonomy is thus to establish a natural classification based on phylogeny *and* phylogenesis.

DOCTRINES

Dialectics: Epistemological doctrine according to which reality is a continuum whose elements are intimately linked to each other. Dialectics is consequently characterized by a systemic approach, considering that a whole can be greater than the sum of its parts (holism, emergentism). Everything that exists would therefore be composed of a single substance (monism) that constantly changes (thus according to Heraclitus "all entities move and nothing remains still"). In its idealistic version reality is therefore a spiritual flow (e.g. Leibniz, Hegel, existentialism), while

in its materialistic version reality is nothing else than the history of the matter, whether this later is considered fully knowable (e.g. Marx, Darwin, Einstein) or not (e.g. Nietzsche, poststructuralism). **Idealism**: Ontological doctrine according to which reality is fundamentally mental or of spiritual nature. In its realist version general ideas are accorded a proper existence outside of the thinking subject (e.g. Plato, vitalism), whereas nominalists see in them only abstract constructions, thus recognizing only particular perceptions as the sole realities (e.g. Berkeley). **Materialism**: Ontological doctrine according to which the ultimate nature of any being is material (e.g. Democritus, mechanism). There are therefore neither spirits nor ideas outside the body, and mental phenomena are explained by a particular organization of matter (physicalism). In its nominalist metaphysical form, experimental refutation is often regarded as the only source of a generally temporary truth (e.g. Popper). Inductive reasoning and use of statistics are instead approved by realists (e.g. Comte, Poincaré) and dialecticians (e.g. Kuhn). **Metaphysics**: Epistemological doctrine according to which knowledge is obtained through analysis of reason (rationalism) and/or of sensory experience (empiricism). Metaphysics thus has a strong trend to consider that everything can be reduced to its parts (e.g. Spencer, Wilson, scientism). This way of thinking also involves regarding movements or changes as disturbances masking the universal and eternal truth (e.g. Cuvier, fixism; according to Parmenides "being is, but nothing is not"). Metaphysicians therefore generally believe that the world is divided into several unassimilable entities (e.g. mind/matter dualism of Plato or Descartes, pluralism of Aristotle's categories). **Nominalism**: Gnoseological doctrine according to which knowledge of reality is partly or totally necessarily inaccessible for experience and our understanding. In its materialist version, science consists therefore only in the study of relationships between the manifestations of reality (phenomena) but must refrains from speculating about the underlying causes (e.g. Locke, Hume, neopositivism, structuralism). In its idealist version, the whole of reality is seen as a pure mental representation, which has the effect of denying the existence of any objective reality outside the subject (e.g. Schopenhauer, Bohr, instrumentalism, constructivism). **Realism**: Gnoseological doctrine according to which reality is plainly accessible to our knowledge. As a consequence, in its dialectical version it rejects the dichotomy phenomenon/thing-in-itself (e.g. Spinoza, Haeckel, Bell, Bohm, naturalism). In the same way, subjects and objects are considered as relative concepts, thus allowing the study of the production of knowledge by scholars as if it were a natural phenomenon.

Table 2. Glossary. I retained a few basic definitions of disciplines and activities discussed in this paper that are not the subject of a formal mathematical definition. The definitions of the philosophical doctrines are exemplified by a few authors (philosophers and/or scientists) and also by some distinctive movements.

Definition 8.1 *(Cladistic Partition)* Let there be g a clade defined in K on the network $G = (X, p)$. The set $\{g_1, g_2\}$ is a cladistic partition of g if and only if g_1 and g_2 are clades such that $g_1 \cap g_2 = \emptyset$ and $g_1 \cup g_2 = g$. Then, both groups are called sister clades.

Observation 8.2 *(Existence)* There does not always exist a cladistic partition of a clade, even if it is composed of several elements.

The problem revealed by this observation is depicted in Figure 17B. It comes directly from Theorem 5.4 according to which a continuous partition of a continuous group (which can be the case

of a clade) necessarily contains at least one paraphyletic group (which can*not* be the case of a clade) if it comprises at least two elements. As it has previously been said, it is impossible to remove *a priori* an ancestor in a cladistic study (whether it is synchronic or not). The ancestral status of a taxon can only be determined *a posteriori* after the examination of all available data (cladistic, palaeontological, ecological, etc.).

Theorem 8.3 *(Uniqueness)* In a network without mergings a cladistic partition of a clade, if it exists, is always unique.

Since mergings are rather rare in evolution of higher taxa then this theorem globally validates the cladistic method for phylogenetic reconstruction. This result should not be nuanced by the existence of horizontal gene transfers (HGT) between branches, particularly among bacteria. Genes and organisms bearing them should indeed not be confused. The goal of phylogenetics is to reconstruct a genealogy of organisms, not of genes (Valas & Bourne 2010). Although these HGT can interfere with evidences of heredity, one must keep in mind that a gene must be copied: it does not grow and does not divide, contrarily to a cell. It is astonishing to have to remind this, but the unit of life is cell, not gene. Confusion may come from the unfortunate term "molecular phylogeny" and some bad popular science papers talking about DNA as a magic molecule containing all the answers to the mysteries of life. By the way, DNA is not alive. Thus, confusing the tree of life with a tree of genes is a kind of vitalism. Then, the relation p should never be read as "x_1 donates genetic material to x_2", as Kwok (2011) misleadingly suggested.

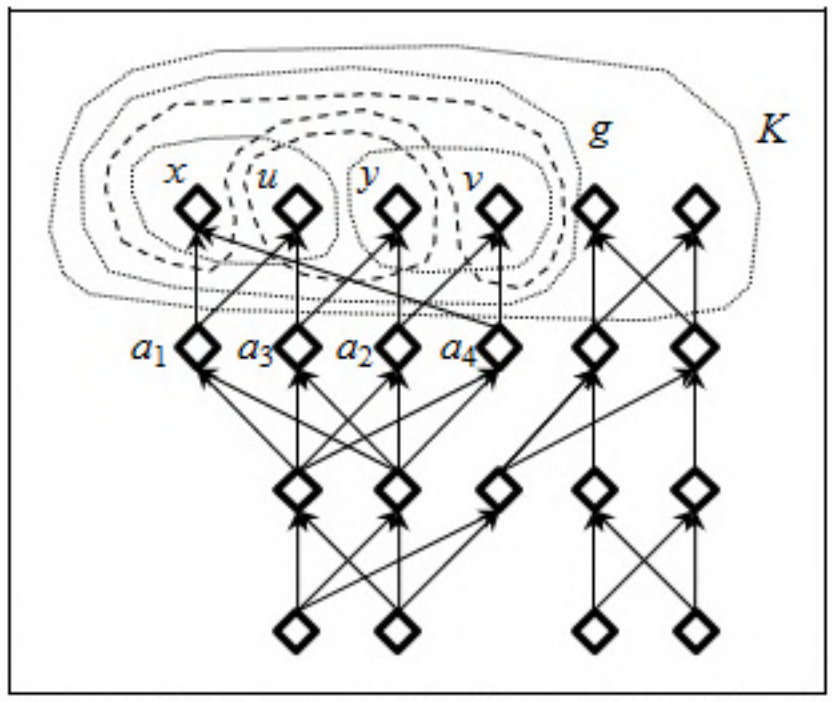

Figure 18. Alternative cladistic partitions in a network with mergings. The clade g defined in K has two different cladistic partitions: $\{\{x, u\}, \{y, v\}\}$ or else $\{\{x, v\}, \{u, y\}\}$.

By opposition, in a network with mergings it is sometimes possible to split a clade into several different cladistic partitions (see Figure 18). This is not a particularly surprising result; it actually corresponds to haplogroups in population genetics. The dividing of humanity into distinct haplogroups is known to have been especially helpful in the reconstruction of its oldest migrations through continents. Globally, networks without mergings can be used as a model for phylogenies in supraspecific levels, whereas networks with mergings are more appropriate as a model for genealogies in infraspecific levels. But it is clear that in reality there exists a continuum between these two situations, there are not of different nature.

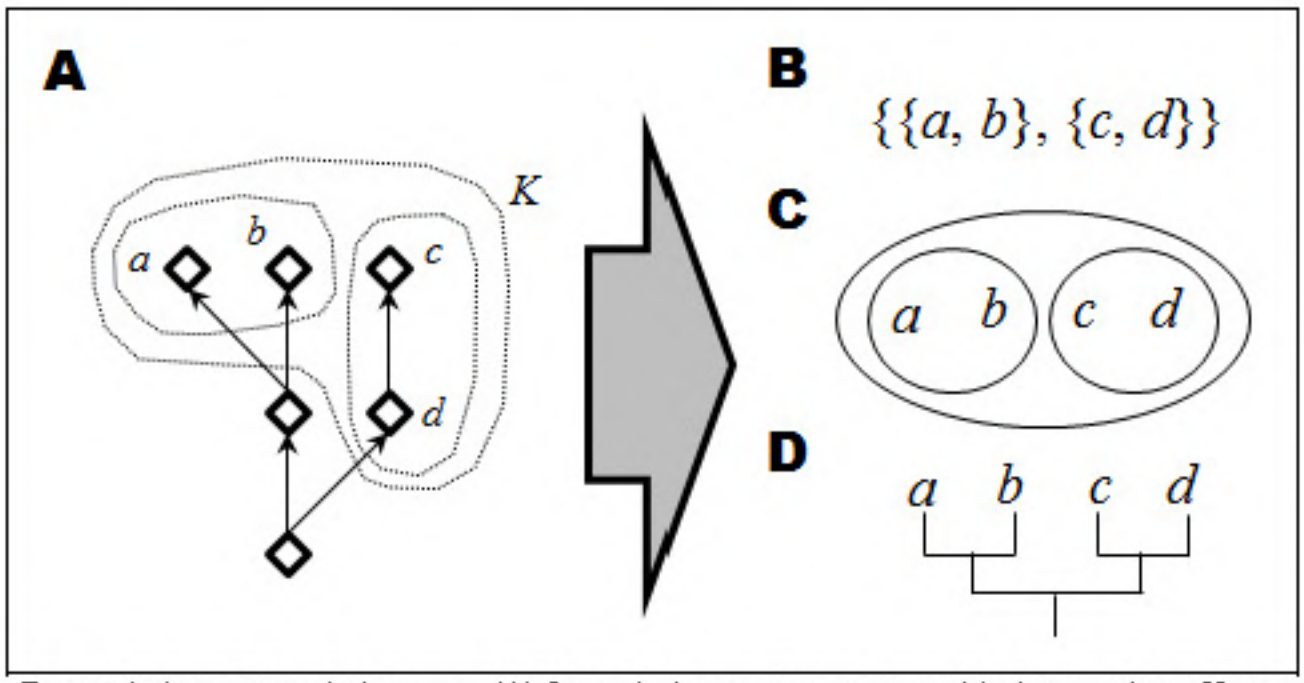

Figure 19. From phylogeny to cladogram. (A) In a phylogeny, we are considering a subset K containing four species a, b, c and d. (B) Clades are embedded according to the formalism of set theory. (C) Venn diagrams are an intuitive form of graphical representation. (D) Cladograms are easier to read, but they have the disadvantage of making one to believe that branches and nodes represent something: they are not genealogical trees.

Definition 8.4 *(Cladogram)* Let there be g a clade in K on network $G = (X, p)$, and $\{g_1, g_2\}$ a cladistic partition of g. A cladogram of g is a set $\{c_1, c_2\}$ such that $c_1 = g_1$ or else c_1 is a cladogram of g_1, and likewise $c_2 = g_2$ or else c_2 is a cladogram of g_2.

A cladistic partition is thus a very simple cladogram. This iterative definition allows representing cladograms as Venn diagrams, thus emphasizing that the branches of cladograms are nothing else but an alternative representation of embedded sets (see Figure 19). These branches does not represent lineages, cladograms are therefore neither genealogies nor phylogenies! Thus, the nodes do not represent ancestors but only higher clades. Finally, clades in themselves do not represent phylogenetic relationships since different processes as the splitting of a mother species into two daughter species or else a daughter species arising from a surviving mother species, lead to identical cladistic representations (see Figure 19). Contrarily to what is sometimes claimed (Martin & Wiley 2010), and although cladograms do have the form of a tree, they are not based on graph theory but only on set theory. The construction of cladograms is the goal of cladistics. We can call cladonomy the naming of the different clades embedded within each other (Brummitt 1997). The result of cladonomy is a cladification, i.e. a cladogram whose nodes are named. But a cladogram is only a preliminary arrangement which must be rigorously interpreted with regard to *all* available data in order to reconstruct the true phylogeny. A simple clade $\{a, b\}$ can be interpreted in five ways (see Figure 20)! Consequently, by Theorem 5.4 and by Observation 8.2, it is clear that a classification of species can be based neither on strict holophyly nor on strict holoclady. Let us recall that another mathematical analysis of these concepts, although based on cladist assumptions, came to a similar conclusion (Kwok 2011).

9. ESTABLISHMENT OF THE CURRENT PARADIGM

The theoretical weaknesses of cladism we have highlighted in previous sections naturally lead us to examine the reasons for its success. Firstly, cladism proposes to directly convert cladograms into ersatz hierarchical classifications by removing a laborious step of expertise to delineate the different potential groupings (Hennig 1966). Secondly this doctrine was shipped with a rigorous and relatively simple method for constructing these very cladograms. And thirdly, ancestors, whose classification was particularly complex, were axiomatically eliminated. This therefore simplified

both phylogenetic and taxonomic work. The quick acquisition of precise and reproducible results, so apparently objective (Hennig 1975), promptly defeated the counter-arguments of traditional taxonomists who insisted on the lack of relevance and realism of these results (Mayr 1974).

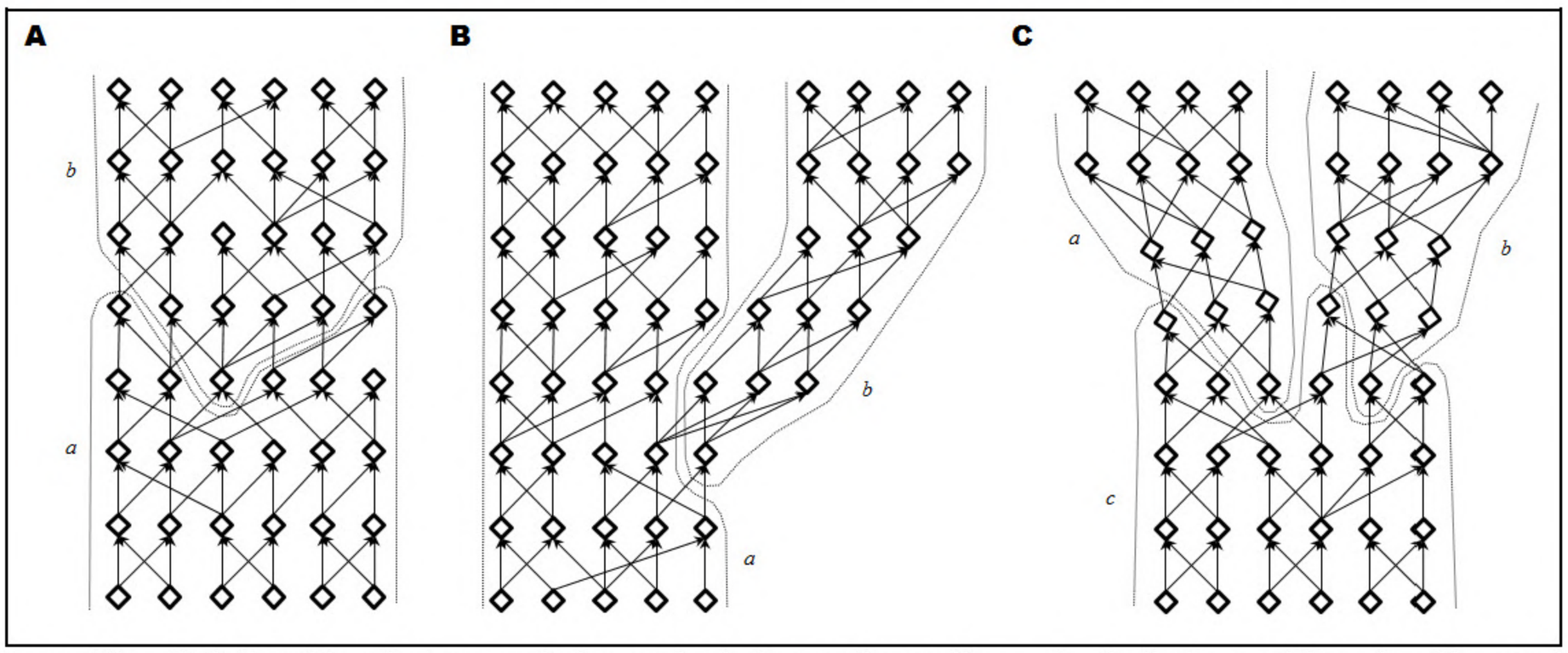

Figure 20. Relationships between clades and phylogenetic reality. A cladistic partition {*a*, *b*} can be interpreted in five different ways. (A) One anagenesis: a mother species *a* turns into a daughter species *b* (or the reverse); this type of speciation is generally sympatric. (B) One cladogenesis and one anagenesis: a daughter species *b* buds from a persisting mother species *a* (or the reverse); this speciation is usually peripatric. (C) One cladogenesis and two anageneses: a mother species *c* disappears by giving birth to two daughter species *a* and *b*; this type of speciation may appear in allopatric contexts.

In a Kuhnian perspective, the period of the years 1960-1970, which saw the rise of cladism, can be called a scientific revolution. The intuition and expertise of a few taxonomists were indeed at the heart of this discipline in the early twentieth century, methods of phylogeny reconstruction were so poorly formalized and principles for deciding between alternative classifications were even vaguer. Systematics was suffering from a poor image and was desperately looking for "scientific respectability" (Dumoulin & Ollivier 2013). This practice through trial and error in restricted circles can be called a pre-paradigmatic situation. The arrival of a rigorous approach with clearly defined aims put an end to it, and brought systematics into a new paradigm, that of cladism. We call "paradigm" a set of opinions shared by practitioners of a discipline that guides researches, permits identification of the problems to be solved, determination of acceptable methods, and judgement about the plausibility of the findings (Kuhn 1962).

A paradigm is a constraining framework of thought, it mainly acts unconsciously and it greatly influences how we interpret experimental data and discourses from our peers. This last point may seriously affect scientific communication when researchers working within different paradigms (often incompatible) try to share their results or theories. Thus, we can read for example in a review of a book of Zander (2013): " 'this book rejects the idea that [...] a clade is necessarily monophyletic' (p. 5). This position is so different from the familiar cladistic perspective that at times I found it difficult to comprehend" (Brower 2014). The problem does not come from the obscurity or the complexity of the topic, but from a real subjective difficulty in understanding concepts that do not belong to the paradigm we are used to (here Zander is only drawing attention, through his own vocabulary, to the existence of cryptic paraphyly in a context of holoclady, see Section 7). I will develop this aspect through two historical disputes.

ONTOLOGY	GNOSEOLOGY	EPISTEMOLOGY	SCHOOL	REPRESENTATIVES
Idealist	Nominalist	Metaphysical	Cladist (pattern)	Ebach MC, Nelson GJ, Patterson C, Platnick NI, Williams DM
		Dialectical	Pheneticist (or numerical)	Sneath PHA, Sokal RR
	Realist	Metaphysical	Essentialist (or typological)	von Linné C, Cuvier G
		Dialectical	Gradist	Haeckel EH, Lamarck JB
Materialist	Nominalist	Metaphysical	Cladist (process)	de Queiroz K, Farris JS, Hennig W, Woese CR
		Dialectical	-	Darwin CR
	Realist	Metaphysical	Evolutionist (classical)	Ashlock PD, Cronquist AJ, Mayr EW, Simpson GG
		Dialectical	Evolutionist (modern)	Cavalier-Smith T, Hörandl E, Stuessy TF, Zander RH

Table 3. Philosophical classification of the main schools of systematics. Philosophy of knowledge can be divided into three fields of study that are about three great fundamental and interrelated questions. Ontology: What is reality? Gnoseology: What can we know? Epistemology: How can we know? (see Table 2) This categorization, which is for educational purposes, is obviously very schematic and do not report the subtleties and inhomogeneities in each school of thought. The few authors presented for information purposes in the last column have been classified only with regard to their *actual* practice of taxonomy, and not with regard to their theoretical statements or practice in other areas of biology. The quality of their scientific work cannot be appreciated at its true value only by their positions (which are approximate) in this table.

As we have previously explained, Ashlock (1971) coined the term "holophyly" to reflect the concept used by cladists under the misleading name of "monophyly". Despite several exchanges around the problem raised by the original article (Nelson 1971; Ashlock 1972; Nelson 1973), it seems that cladists involved in this dispute never understood that Ashlock's remarks were purely nomenclatural, his aim was that supporters of both schools could argue their views without being confused by unnecessary terminological quarrels (Vanderlaan et al. 2013). While one might naively interpret the attitude of Nelson as ill will, the analysis of his words allows us to understand that what he meant by "monophyly" is actually the concept of holoclady. Similarly the distinction between what he calls "paraphyly" and "polyphyly" corresponds in fact to different degrees of heteroclady. Since the concept of monophyly *sensu* Ashlock encompasses both the holophyly and paraphyly, Nelson could only have imagined that Ashlock aspired to a word encompassing both concepts of holoclady and heteroclady, which is clearly useless… Hence the misunderstanding and the extension of this terminological controversy.

One of the characteristics of a paradigm striving to impose itself is looking for support from major scientific figures. This often takes the form of a re-interpretation of texts written by famous and established authors. They are then considered as precursors of the new paradigm, thus allowing their authority to redound to it. Thus, it is common to find in the cladist literature statements such as

"Darwin was very clear that genealogy should be the only criterion of classification" (Padian 2004). Although it is anachronistic to make Darwin an adherent of one of the two schools of classification born in the mid twentieth century (Padian 1999), such a conclusion still seems to favour Darwin's interpretation as a precursor of Hennig and cladism. The problem stems from the cladist view that today's scientists take on the meaning of the vocabulary used by Darwin. It is clear in particular that the word genealogy has radically changed its meaning in the meantime: firstly Darwin did not have at his disposal the term "phylogeny" coined later by Haeckel, and secondly cladists now tend to use this very word to refer to the sequence of dichotomies in a cladogram. Thus, it can be read:

"I believe that the ARRANGEMENT of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural; but that the AMOUNT of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders." (Darwin 1859)

Although the first part of the sentence seems to go in the direction of a "pre-cladist" interpretation, the second part leaves very little doubt as to Darwin's view about importance of the degree of similarity in the making of a classification as natural as possible (Mayr & Bock 2002). Statements like "Darwin never endorsed similarity as the other half of a 'dual criterion,' " (Padian 2004) are therefore at best highly dubious. When cladists read that a classification "must be strictly genealogical" they understand most of the time "holophyletic". When Darwin wrote that a classification "[should] be strictly genealogical" he probably only meant "monophyletic" and was certainly not much concerned about paraphyly. Our Theorem 6.2 states by the way that phylogenies are genealogies. From this point of view, it is quite possible for an evolutionary taxonomist to say that genealogy alone does give a classification! Anyway, it is once again important to note that in Victorian era the problem of phylogenetic reconstruction was in its infancy, which explains that in practice the classifications established by Darwin were only based on phenetic criteria (see Table 3). We may eventually regret a too metaphysical reading of this issue by some evolutionists (Mayr 1974; Mayr & Bock 2002) who see in it the use of a "dual criterion," genealogy and similarity, whereas in Darwin's mind, similarity (or "affinity") was actually a reflection of genealogy.

10. ANALYSIS OF THE CLADIST DOCTRINE

Cladism as it was founded by Hennig is based on three key assumptions. The first is that cladograms' nodes do represent real speciation events through splitting (Hennig 1966; see Figure 20C). The second is that it is extremely unlikely, given the continual transformation of the living world and the vagaries of fossilization, that a species we know is the ancestor of another one. Even if by chance this ever happens, it would be anyway impossible to prove this parental link. The third, more implicit, is that the evolution of species is occurring at a more or less constant rate (uniformitarianism, not to be confused with actualism). This would imply that the more recent is the divergence between two species, the more similar these two species are. Clades would therefore be the kind of groups with the maximum content in phenetic informations.

10.1. Structuralist Influence

The presumed speciation mechanism requires taxonomists not to consider any species as ancestral to another one, and thus to classify them only as sister groups. This dogma according to which reality is not accessible to us is characteristic of a *nominalist* philosophy of knowledge: science aims to model and predict manifestations of reality but not to understand reality itself. The ordering system advocated by Hennig (his "phylogenetic classification") is thus more a reflection of our knowledge of manifestations of reality (distribution of characters, fossils, etc.) than a theory *of* reality. However, this is not a radical kind of nominalism which would imply that reality is entirely

unknowable, or even that it does not exist. Hennig did recognize the material nature of reality and its independence of the subject. This can be seen through his attachment to the fact that successive branchings of cladograms do represent an evolutionary process. This is clearly a *materialist* position.

Finally, the Hennigian conceptual framework can be described as *metaphysical* since it is both rigidly static and reductionist. Indeed, its phyletic arrangement does not reflect any transformation (no species becomes another, no group emerges from another group, etc.) and is reduced to represent only the structure of the process supposed to be at work (the splitting of a mother species into two daughter species). In this regard, it is significant to note the almost complete disappearance of the concept of phylogenesis in our current practice of systematics. Coined by Haeckel (1866), the term "phylogenesis" refers to a real *developmental process* ("Entwickelungs-Vorgang" in the original) that must be contrasted with the term "phylogeny" coined later (Haeckel 1868) which refers to a reconstructed *history of the development* ("Entwickelungsgeschichte" in the original). This opposition is more or less of the same kind as our modern *process/pattern* opposition, even if this vocabulary was coined later (Dayrat 2003).

To understand the history of science it is essential not to naively conceive it as a fully autonomous entity developing only through gradual accumulation of observations and refutation of increasingly efficient theories. Science is not independent of the society in which it operates; it is a byproduct of it. As such, its practice is subject to the various ideologies that have impregnated society. Systematics is no exception to this trend, which enables us to examine the cladist dogma in the context of its time. Yet, among the modern philosophies of knowledge, both materialist and nominalist, and having a metaphysical method (see Table 2), the main general school is *structuralism*: science then aims to discover the intrinsic structures of the manifestations of reality while refraining from speculating about its nature or the underlying mechanisms. The structuralist movement (emphasizing synchronic structures rather than diachronic causes) emerged in the early twentieth century in the field of linguistics and has then greatly influenced many other scientific disciplines. In physics for example it gave birth to the *instrumentalist* school, which culminated with the so-called Copenhagen interpretation of quantum mechanics (Nikolic 2007). This relationship between structuralism and cladism has already been raised by other authors (Grande & Rieppel 1994; Zander 2011).

10.2. Paraphyletic Species

If the speciation mechanism envisaged by Hennig were correct, it would imply that absolutely all extant species should be holophyletic. However, speciation by splitting is a complex mechanism that requires the occurrence of two divergent anageneses immediately after an event of cladogenesis (see Figure 20C). It is much more likely that species originate mostly by simpler mechanisms (Mayr 1974) such as direct transformation of one species into another (see Figure 20A) or by budding of a single daughter species from a mother species (see Figure 20B). It is ironic that cladistic analysis (and cladism in general) is largely based on the principle of parsimony, while the axiomatic existence of an unobserved mother species giving birth to the two observed species appears as a superfluous hypothesis! A hypothesis even more flawed since the mother species is not only unobserved, but by definition *unobservable*, which logically makes it both unverifiable and irrefutable. In fact, it is estimated that about 20% of extant species of plants and animals are paraphyletic (Rieseberg & Brouillet 1994; Crisp & Chandler 1996; Funk & Omland 2003; Crawford 2010; Schmidt-Lebuhn et al. 2012; Ross 2014).

It is hardly surprising that cladists have adopted a very formal concept of species, but also a very fanciful one, allowing among other things getting around this problem. This so-called "phylogenetic" concept of a species conceives it as a lineage between two events of cladogenesis (or extinction). The problem is that it is an artificial criterion that completely ignores the possibility of

anagenesis within the same lineage, and also paradoxically ignores the possibility of an absence of anagenesis in one of the two daughter lineages (budding mechanism). This purely conventional definition does not correspond to biological reality (while the goal of biology is precisely to describe and explain this reality), and is much less relevant than alternatives based on empirical properties of species: reproductive isolation (for eukaryotes only), ecological cohesiveness (within a restricted adaptive zone), morphological similarity, etc.

But we should not see them as competing definitions; all these properties are actually dialectically related to each other. For example, morphological similarity results from both stabilizing selection in a certain ecological niche, but also from genetic recombination through sexual reproduction. But the fatal flaw of the phylogenetic species concept is that it is not even logically consistent, which is revealed with force if one tries to rigorously model it using mathematics(Velasco 2008). One could be tempted to see in this matter an idealist drift of Hennigian nominalism, since instead of trying to organize empirically observed phenomena it attempts to integrate them into some aprioristic categories, non-amendable through experience (like the concept of "phylogenetic" species). This does have the advantage of allowing researchers to work with very precise concepts, because aprioristically devised, but they are too often simplistic, or even frankly irrelevant. It is profoundly unreasonable to replace imprecise but relevant concepts by precise but irrelevant ones.

10.3. Virtual Ancestors

The second postulate of cladism concerns the non-fossilization of ancestors, or the impossibility to formally recognize them as ancestors, is empirically false (Prothero & Lazarus 1980; Paul 1992; Benton & Pearson 2001; Prothero 2009). In simple terms, if two morphologically slightly different fossil species succeed each other in two adjacent geological layers, the simplest and least costly hypothesis is that one is descended from the other (parsimony). In absence of evidence suggesting an alternative scenario, it is unnecessary to systematically admit the existence of a third species, of which we have no vestige, and which would be the mother of the two observed fossil species. The first assumption is verifiable or refutable depending on whether subsequently discovered evidences are consistent with it or not, while the second hypothesis is neither verifiable (since the discovery of a third fossil ancestral to the first two would automatically be interpreted, in a cladist framework, as a sister species of the other two) nor refutable (since the hypothetical ancestor is unobservable). It is quite surprising in this regard that in its efforts to establish itself as a new paradigm, cladism heavily relied on the philosophy of Popper (Rieppel 2008; Vogt 2014), and in particular on its highly prescriptive falsificationism which specifically prohibits the consideration of such irrefutable assumptions.

In addition, if a fossil or living species may be paraphyletic, why not a genus, or a family, or an order, etc.? Two options are open to cladists. The first is to abandon species as the base unit for their phyletic arrangement to finally class only individual organisms into clades without ranks. It is therefore rather difficult to talk about a "natural" arrangement. The second option is to take into account the biological reality of species by restricting their fight against paraphyly only to higher levels of the classification. The first solution is clearly a radicalization of nominalism (thus tending towards an idealist nominalism), while the second one is just an adjustment preserving materialism. But, is holophyly sufficient for guaranteeing the naturalness of taxa higher than species (genera, families, orders, etc.)?

10.4. Uniformitarianism and Punctualism

It is rather clear that cladists see paraphyly as an artificial cut making clades incomplete and therefore unnatural. But what is truly meant by "natural"? Even before the publication of the *Origin of Species* (Darwin 1859), naturalists of the Victorian era shared the view that the Linnaean classification reflected real relationships of "affinity" between organisms. The origin of this affinity,

which allowed the constitution of nested groups, was then unknown (Winsor 2009). As we know, Darwin proposed that this mysterious affinity was in fact the expression of common ancestry, and then that a natural classification had to be genealogical. Does our classification still reflect such an affinity today? Trying to answer this very question involves defining the concept of affinity without referring to either genealogy or evolution; we might otherwise produce a circular reasoning. Thus, according to Gilmour (1937), a natural classification is an "arrangement of living things which enables the greatest number of inductive statements to be made regarding its constituent groups, and which is therefore the most generally useful for the investigation of living things". That is to say, naturalness means maximizing the *overall similarity* of organisms within groups thus formed, while minimizing it between these very groups. It is indeed such a principle that taxonomists used to follow before the introduction of cladism.

The problem that arises here is the apparent discrepancy that often exists between the degree of kinship and the overall similarity (Mayr 1974; Ashlock 1979). Thus, although crocodiles are phyletically closer to birds than to lizards, it is indisputable that the predecessors and contemporaries of Darwin did wonder about the affinity they noticed between crocodiles and lizards, not between crocodiles and birds. Contrary to what states the third postulate of cladism cited above, the pace of evolution can greatly vary (Eldredge & Gould 1972; Gould & Eldredge 1977; Cavalier-Smith 2006; Cavalier-Smith 2010a; Zander 2010). It may be argued that the morphological differences that we perceive are in fact very superficial; organisms that look alike might actually be quite different from a molecular point of view, and *vice versa* (Schmidt-Lebuhn 2014). Indeed, only a small part of a genome is actually involved in coding the macroscopic phenotype. The goal of taxonomy remains however to classify organisms and not just their genomes. Otherwise we would believe that organisms can be reduced to their genomes, which is a mark of a flagrant reductionist reasoning, as if phenotype were only the rough expression of genotype that would then be the true essence of the organisms we wish to classify. This is not very far from a kind of *essentialism*, a notoriously outdated philosophy.

Moreover, it is now established that molecular characters can also undergo some very abrupt evolutionary accelerations (Shavit et al. 2007). In practice, molecular phylogeneticists are well aware that in order to reliably resolve phyletic relationships between distant organisms one must try to eliminate the parts of the genome that have irregularly or quickly evolved for statistical reasons. What interest would it have to classify organisms solely on the basis of molecular variations that have no functional impact and therefore no adaptive value? If these characters are actually valuable to reveal phyletic relationships, they are however of no value for us to make predictions about the body plan, the physiology and the ecology of an organism; see for example George (2014) for a concrete case. Consequently we can now read all over, in scientific literature and its popularization, some absurdities such as man *is* a bony fish (Brummitt 2006). Following the same reasoning (Aubert 2013) we will soon have to say that man *is* a bacterium, the latter being paraphyletic even if one excludes archaebacteria: "Most papers [...] make this very mistake by treating eubacteria as holophyletic, whereas they are almost certainly paraphyletic" (Cavalier-Smith 2010a); see also Jékely (2007) and Cavalier-Smith (2014).

Darwin's *descent with modification*, which is the heart of the genealogical explanation of affinity, actually covers two contradictory principles: heredity and variation. The first explains why two organisms with a common ancestry may (not "must") exhibit a certain affinity while the second explains why they may not (not "must not"). It is *natural selection* (stabilizing or directional selection, or genetic drift) that realizes these potentialities. Affinity reflects therefore the whole Darwinian evolutionary mechanism (not just the topological aspect of genealogy). Instead, cladism tacitly relies on an *uniformitarian* (metaphysical) reading of Darwinian gradualism, while the latter was rather a precursor of modern *punctualist* gradualism (which is dialectical, not to be confused with

saltationism which is also metaphysical). Thus, everything leads us to believe that there is a strong conceptual relationship between the principle of parsimony used in the original cladistic analysis and the rejection of paraphyly. However, as an evolutionary model, the principle of parsimony is empirically false; it notoriously leads to an artefact called long-branch attraction (LBA), thus forcing systematists to develop methods of phylogenetic reconstruction based on more complex evolutionary models and superior statistical analyses (e.g. Bayesian inference).

10.5. Idealist Drift

Empirical objections we can oppose to cladism are likely anomalies within this paradigm. However, a paradigm would not be a paradigm if it were wobbling when facing any difficulty. Besides sociological reasons I will not detail (authority of old scientists, marginalization of non-conformist scientists, psychological and political tensions, etc.), there are also objective reasons that explain the resistance of a paradigm to change. Thus, the deep philosophical and taxonomic decline caused by the advent of cladism was accompanied by a revolutionary progress, through the mathematization it made possible, in phylogenetic techniques. The efficiency of this system thus makes the possibility of its refutation somewhat extraordinary, which then requires a stack of extraordinary evidences. It is actually less costly to simply ignore the anomalies or to adapt to it by amending the paradigm with *ad hoc* hypotheses (at least to some extent).

In the first case we deal with traditional cladism (called process cladism), now mainly represented by numerous molecular phylogeny papers that simply (in a reductionist framework) classify genomes instead of classifying organisms. In the second case we have a minor kind of neocladism (called pattern cladism) that radically rejects any kind of realism and defends the idea that cladistic analysis and cladist arrangement that follows can be aprioristically justified without referring to any theory of evolution or any evolutionary model. Since characters are not weighted, then some of the early cladists, but not Hennig (1966), denied that the cladistic analysis was based on an evolutionary model (Farris 1983). This way of introducing impervious and fundamentally opposing categories (i.e. with or without weighting) is a typical metaphysical thinking. Yet, as rest is not the opposite of movement, the so-called "absence" of weighting is actually an equal weighting, thus undeniably making it an evolutionary model (unfortunately empirically false).

While conventional cladists have long acknowledged this fact by developing more complex evolutionary models, neocladists still try to deny it by rejecting theory of evolution as foundation of cladistic methods. The main line of defence of this position is simply that the principle of parsimony allows an optimal "classification" in terms of information content from a matrix of character states (Brower 2000). That the arrangement is optimal is one thing, but that history matches this very arrangement is another (Felsenstein 1978). Thus, the application of the principle of parsimony (in phylogenetics) to reconstruct the actual evolutionary history is rationalized only through its classificatory properties (in taxonomy). This serious confusion between taxonomy and phylogenetics (see Table 2) leads *de facto* to a purely descriptive arrangement without any historical relevance. It is then not surprising that some systematists did not hesitate to connect pattern cladism with pheneticism (Halstead 1980; Ridley 1983).

This singular philosophy inevitably gave birth to new cladistic methods such as the famous three-taxon analysis (Nelson & Platnick 1991). This strategy of "phylogenetic reconstruction," which treats individually each character for each possible group of three species, results in minimizing the number of homoplasies while traditional cladistic analysis results in minimizing the number of necessary transformations on an optimal tree (Marques 2005). This does well maximize the information content of the groups thus reconstructed, but fails to distinguish synapomorphies (shared derived characters) and symplesiomorphies (shared ancestral characters). The obtained groups are therefore not clades! It is hardly surprising that a method so remote from biological transformism has

been strongly criticized by conventional cladists (Farris & Kluge 1998) and even considered an idealist abuse of the principle of parsimony (Harvey 1992). Philosophy of pattern cladism originally aimed at justifying traditional cladistic analysis independently of any evolutionary model, but since existence of evolution is not recognized then it fails to group species according to their synapomorphies (Farris 2012). This leads to a most ironic situation: some pattern cladists go up to confuse homology and synapomorphy ("symplesiomorphy and synapomorphy are no longer necessary terms: only homology has any evidential value"; Ebach et al 2013), which did not fail to be immediately regarded as a disguised reintroduction of paraphyly in taxonomy (Farris 2014).

As admitted by its own supporters, neocladism is a kind of renunciation of phylogenetic reconstruction: "relative relationships, in the sense of sameness or homology, are better ways to classify and summarize overall taxic relationships than inferring genealogies or phylogenies" (Williams et al. 2010). Such a divorce between taxonomy and phylogeny may seem surprising from biologists yet recognizing transmutation of species (transformism). But this recognition is actually purely formal: "Pattern cladistics was — and still is — a reaction against transformational 'phylogenetics', be that of taxa (Ernst Haeckel) or characters (Willi Hennig, numerical cladists, etc.)." (Williams and Ebach 2008). This neocladism, ostensibly anti-transformational, is therefore an heir of ancient Eleaticism and logically reached the same fixist paradoxes, such as the famous stationary flying arrow (at any instant a flying arrow occupies a space equal to its volume, yet since movement is a change of position then the arrow is always at rest…). Prophetically, pattern cladism was rightly connected to the fixist metaphysical idealism of Agassiz (Rieppel 1988) even before the controversy about three-taxon analysis.

10.6. Pitfall of Nominalism

Cladism, as a kind of nominalism, categorically forbids speculation about entities considered as unobservable. Hypothetical common ancestors located at cladograms' nodes are such entities (since cladograms are not genealogies). Therefore, they do not correspond to any diagnosable species. Thus, if an ancestor species of a taxon were revealed to us, we would have to represent it as a sister clade and not as a node (Nelson 1973). So we can consider that kinship relations depicted by cladograms are either ambiguous (see Figure 19) or purely fictional (see Figure 20). As in a family, there is the same degree of kinship between a mother and her daughter as between two sisters. Yet the relationships between a mother and her daughter or between two sisters are fundamentally different from a historical perspective. It is often argued that cladograms depict sisterhood relationships rather than ancestor-descendant relationships (Lecointre et al. 2008), but it's wrong! As we have shown, cladograms are simply unable to distinguish a relationship between sister groups from a relationship between ancestor and descendant. From this point of view it seems extremely difficult not to find contradictory that a "classification" that so poorly reflects evolutionary history really at work considers itself an heir of Darwin's genealogy and even describes itself as "phylogenetic".

But perhaps we could better understand this matter by briefly examining entities that cladists believe they class. Hennig indeed reduced organisms to "semaphoronts," that is to say bearers of characters. As such, cladists do not class real organisms, but only abstract matrices of characters. The problem is not the manipulation itself of simplified representations of organisms, but the lack of return to reality (which would be "speculative" for anti-realists). So we end up with purely descriptive results, devoid of any explanatory power. The refusal of seeking to infer a real relationship (history) between real entities from abstract links between ideas is a classical pitfall of nominalism: it radically fails to formulate theories because a theory is an explanation of reality. A cladogram is therefore not a theory, but a simple descriptive model (this type of model is generally a preliminary step before the formulation of a theory, while a predictive model is a simplification of a pre-existing theory in order to obtain exploitable predictions). It is particularly important in science

not to confuse a map and the territory it represents; cladist nominalism yet fall into this trap paradoxically because of its negation of the territory. It is rather difficult to reason correctly about a map that does not represent anything real, which effectively leads to terrible phylogenetic speculations totally disconnected from any plausible biological mechanism, as it is the case for example with regard to the various merging scenarios between archaebacteria and eubacteria to explain the origin of eukaryotes (Poole and Penny 2007; Forterre 2011). Philosophy of taxonomy has therefore serious consequences on the progress of phylogenetic research.

10.7. Evolutionist Solution

Could the phyletic arrangement of cladists still be the least bad option available? To argue that this is not the case I will try to briefly dispel the main criticism that has been formulated against evolutionary systematics, namely its alleged subjectivity and lack of reproducibility, or even its informational ambiguity (Hennig 1975). Thus, different evolutionists would supposedly produce different classifications because of the arbitrary emphasis they would put on a particular character. Yet it is well known that characters do not all have the same phylogenetic value. Some very labile ones cannot be used for example to define higher taxa. However, this criticism affects much more Linnaean essentialism rather than modern evolutionism which is based on *overall* similarity to delineate taxa on a phylogenetic tree. This overall similarity is sometimes accused of being an ill-defined concept, thus ignoring decades of development of pheneticism (Sneath 1995) and also deluding oneself about the profound phenetic nature of pattern cladism, and three-taxon analysis in particular (Farris & Kluge 1998; Marques 2005; Farris 2014).

Unlike cladists, the method of argumentation of classical evolutionists was not numerical. However, the presence of numerical values does not guarantee the scientificity of a discourse (otherwise numerology should be considered a science!). One can ask whether the criticisms against classical evolutionary systematics do not come from an illusion of precision due to the use of mathematical tools in cladistic analysis… Anyway, it is important to note that the practice of evolutionary systematics is no longer the same as it was during the first half of the twentieth century. In phylogenetics, it successfully integrated the tools of traditional (morphological) cladistic analysis and also Bayesian (molecular) statistical analysis (Stuessy 2013). Progress has also been made in the field of taxonomy. For example, a reinterpretation of the results of phylogenetics, especially discordant results (Zander 2014a), has allowed the delimitation of precise paraphyletic groups from certain types of heterocladies (Zander 2009). As another example, we could cite the statistical algorithm that has been successfully used so as to objectively delineate island divergent genera derived from continental ones (Stuessy et al. 2014). New tools such as patrocladistics have also been proposed to allow a more objective and more reproducible delineation of paraphyletic groups (Stuessy & König 2008; Stuessy & König 2009; Hörandl & Stuessy 2010). This latter method has for example been successfully applied to angiosperms (Willner et al. 2014) from the raw data of APGIII. This allows the representation of evolutionary theories as true phylogenetic trees (Zander 2014b; Zander 2014c; Zander 2014d) variously called caulograms, phylograms, Bessey's cactus, bubble or spindle diagrams.

Still, evolutionary classifications remain accused of not accurately representing phylogenies because it is not possible to infer phylogenetic relationships between taxa from a classification alone (Hennig 1975). For example it is not possible, from the classification of tetrapods into four classes (Amphibia, Reptilia, Aves, Mammalia), to deduce that birds and mammals are descended from reptiles and that they are themselves descended from amphibians. The phyletic arrangement, that is called a cladification, allows instead the immediate reconstruction of relations between sister clades (yet, as we have previously shown, these relations are *artificial*, i.e. not historically natural relationships but abstract kinships). In addition, this reasoning is based on the assumption that it is desirable to identify phylogeny with classification, which is not the case! A phylogenetic tree and a

classification are in fact two complementary representations of a same evolutionary theory: "they are different ways of abstracting from and representing biological relationships" (Cavalier-Smith 1998). A cladification is thus isomorphic to a cladogram whereas a classification is consistent with a phylogeny; both must be presented together.

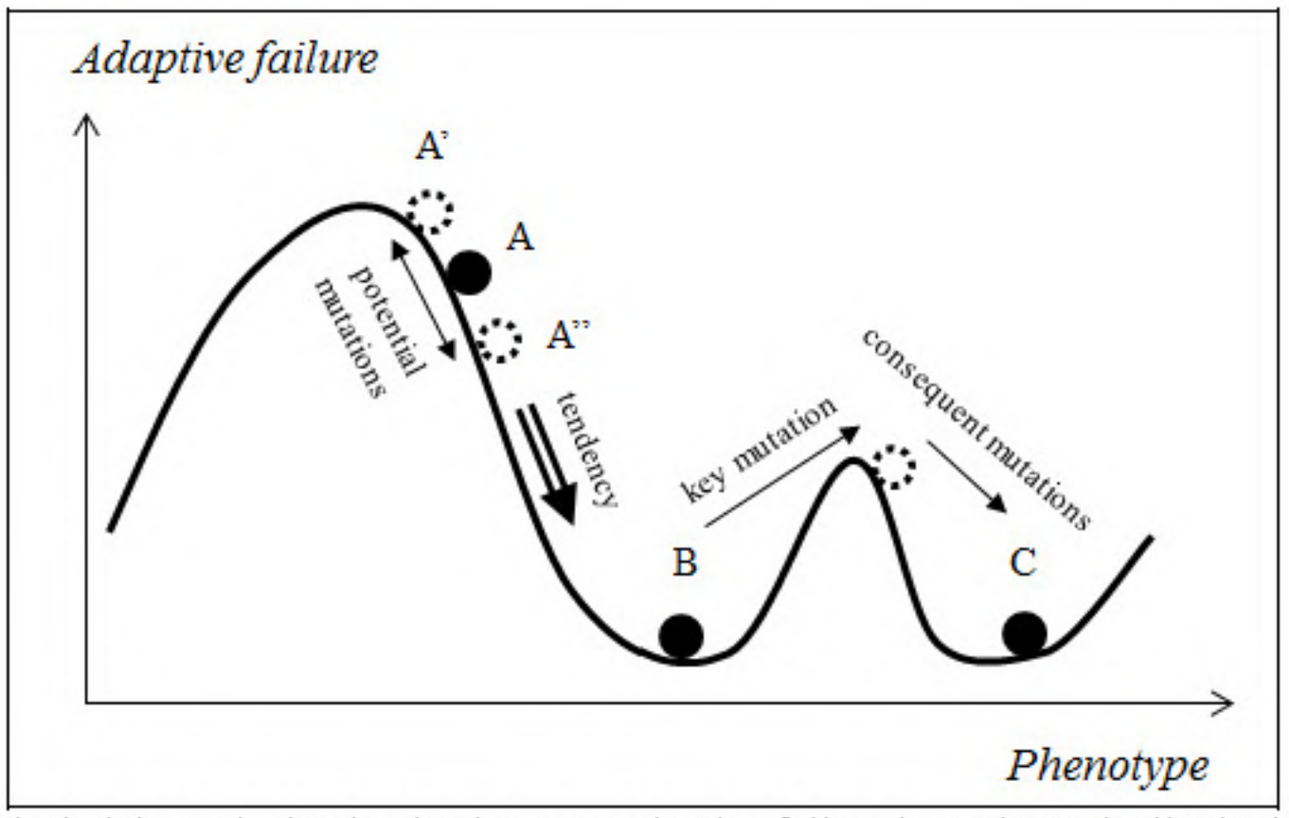

Figure 21. Ecological niche and adaptive landscape. Adaptive failure is mathematically the inverse of adaptive success, or *fitness*; it can be perceived as being analogous to potential energy in physics. Thus, although the phenotype of a species A can randomly evolve towards A' or A'', the better fitness of A'' indirectly causes the emergence of a trend towards an evolution into a depression of the adaptive landscape (ecological niche). A change of ecological niche generally requires the introduction of a key mutation, in the absence of which natural selection would have a stabilizing effect (B, evolutionary stasis). This mutation is not necessarily of extraordinary magnitude (macromutation), like key species in ecosystems, which are rarely the most abundant ones. The population who inherited this mutation then underwent directional selection that will make them reach a new evolutionary optimum (C). If cladogenesis occurs after the key mutation but before subsequent mutations, we will probably see the realization of a case of parallelophyly, a special case of polyphyly where phyletically very close species undergo evolutionary convergence (which explains by the way Vavilov's law of homologous series). It is also worth mentioning that the adaptive landscape is not immutable: its shape can change over time because of the interactions between a species and its niche, the interactions among different ecological niches or even because of a sudden catastrophe.

Ambiguity of information content in taxa is also attacked by cladists, who see this only as disparate criteria concerning ecology, morphology or genetics. How to tell if two species were grouped in the same taxon as a result of high genetic proximity or because they share the same ecological niche? The kind of information that a user could draw from a classification would therefore not be predictable. The predictive value of an evolutionary classification however relies precisely on its probabilistic nature. Blaming overall similarity for its inability to establish a guaranteed subset of characters shared by all members of a group is in fact a criticism from an *essentialist* perspective. In this sense, since groups defined by cladonomy are based on immutable synapomorphies, it is not difficult to argue that cladism is a form of *historical essentialism* (Griffiths 1999; LaPorte 2004). It is by the way a kind of essentialism empirically refuted given potential reversions, which makes all things considered rather suspect the supposedly better predictability of phyletic arrangements. In any case, the accusation of unpredictability precisely rely on the (nominalist) belief that a classification cannot contain information other than those used in its development. But the goal of evolutionary systematics is indeed to infer new information from the collected data, not just to produce a heterogeneous amalgam. This new information is of purely *phylogenetic* nature, it does not match any of the types of data that were used in its production. Only a dialectical thinking

can help us to understand the phenomenon of emergence, i.e. the fact that the whole (classification) cannot be reduced to the sum of its parts (raw data).

Then, phylogenetic information means that two species belong to the same taxon because of an evolutionary leap (a more or less great qualitative leap depending on its rank) that separates them from other species. This leap should not be understood in a metaphysical manner (macroevolution and microevolution are of the same nature!) but in a dialectical manner, i.e. it is the result of an accumulation of quantitative changes that allows us to describe the moving surface of the adaptive landscape with which organisms constantly interact (see Figure 21). So it makes no sense to evaluate a purely *phenetic* distance between two organisms regardless of their natural environment (which is the idealistic mark of pheneticism). Individual characters have to be weighted in terms of their evolutionary significance, which is itself a synthesis of their adaptive value and their evolutionary lability. This classification may be used as a support to explain life history thanks to the view it enables regarding *stasis* within niches and *revolutions* between niches through key innovations (which are not necessarily macromutations!) that give rise to new higher taxa. Classification does not directly represent the phylogeny (pattern), but in a sense leaps within phylogenesis (process).

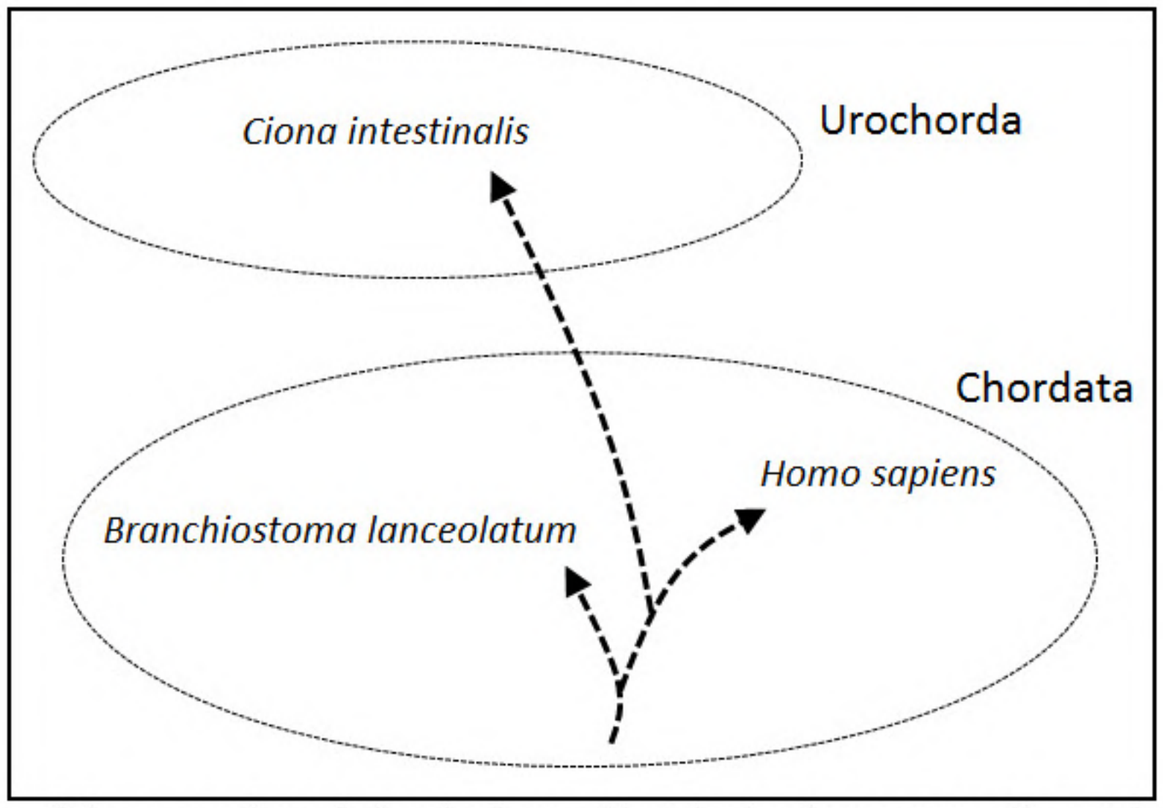

Figure 22. Phylogeny of three species of chordonians. Vertebrates have generally retained the ancestral body plan of cephalochordates while urochordates have radically changed according to a sessile lifestyle. Time is not depicted. Drawn after the classification of Cavalier-Smith (1998).

Finally, I would like to illustrate a particular kind of subjectivity of which evolutionary systematics is accused: anthropocentrism. According to this thesis, cladism would be the only philosophy able of performing the "Copernican revolution" that shall depose man from the top of the evolutionary tree (Lecointre et al. 2008). The concept of *grade* (Huxley 1957; Huxley 1958; Huxley 1959; Cavalier-Smith 1998), largely used by evolutionists, would supposedly refers to the mediaeval notion of "chain of being" (or *Scala Naturæ*). Yet, evolutionism has broken away from Haeckel's and Lamarck's gradism since a long time ago! The concept of *grade of organization* simply refers either to overall similarity (classical evolutionism), or to adaptive zone (modern evolutionism). There is no superior or inferior grade in absolute terms, but only with respect to time. A simplification of body plan because of a shift to a parasitic lifestyle must therefore be understood as a change towards a superior (i.e. later) grade. It is also precisely in this manner that the concept of *grade of character* is perceived within the classical cladist paradigm (process cladism) when ancestral states are distinguished from derived states. In infrakingdom Chordonia (Cavalier-Smith 1998), the phylum Urochorda is therefore placed at the top of the tree instead of the phylum Chordata (to which man

belongs, see Figure 22). Ironically, placing man below yellow sea squirt is a much more drastic Copernican revolution than considering them equal!

CONCLUSION

Contrary to what some may think (Farris 1985), the problem of the meaning of the word "monophyly" is not a superficial terminological quarrel. Without an adequate scientific vocabulary it is unreasonable to hope to properly handle the concepts of systematics and their properties. I have shown that the term "monophyly" should be retained in its Haeckelian meaning firstly for a historical reason (it is its original meaning, see Section 2), secondly for a utilitarian reason (a term uniting both paraphyly and holophyly is indeed necessary, see Section 4) and thirdly for a morphosemantic reason (this meaning is the most consistent, see Section 5). Cladists may substitute the term "monophyly" by "holophyly" without the slightest drawback, so there is no need to continue the defence of the Hennigian meaning of "monophyly" if not solely to prevent evolutionists to express themselves!

My mathematical analysis has shown the many logical inconsistencies that dot the cladist practice, such as the inability to cut a holophyletic group into two holophyletic groups (Theorem 5.4). These theoretical flaws come from a defective philosophy that I identified as firmly nominalist and metaphysical (see Table 3), but fluctuating between materialism (process cladism) and idealism (pattern cladism). This combination is indicative of the influence that structuralism have had on the systematics (Zander 2011). Cladism is therefore unable to adequately reflect some empirical facts like the many paraphyletic extant species. Thus the assertion that no extant species is descended from another extant one is frankly dogmatic. In addition to its intrinsic taxonomic flaws, cladist philosophy leads to some abuses in the practice of phylogenetics. One may note for example the development of a kind of mysticism about horizontal gene transfer (HGT) that supposedly justifies the assertion that "there is no tree." Such a reasoning necessarily confuses genes with organisms that bears them, it is therefore a very rough reductionism (Valas & Bourne 2010). Evolutionism, unlike cladist paradigm, is characterized by a strongly realist and materialist philosophy, which is even dialectical in its most modern (i.e. quantitative) version. Far from being seen as a constraint that should be accommodated, paraphyly is at the heart of evolutionary mechanisms for evolutionism (Hörandl & Stuessy 2010; Hörandl 2014). However, the acceptance of a new way of doing things requires actual papers published using a convincing evolutionist methodology. That's why I will focus in the future on treating real data with the various methods proposed so far in order to test and find the best one, and let the other systematists to judge on results.

It is quite clear that cladism and evolutionism are in fact the modern heirs of two fundamental philosophies confronting each other since ancient times: respectively Eleaticism and Heracliteism. It would be vain to believe that a fight that lasted for 25 centuries can be suddenly completed. Regarding systematics, it would certainly be more advantageous to seek to develop neutral nomenclatural rules, flexible enough to be compatible with both schools, unlike the infamous *PhyloCode* (Keller et al. 2003; Rieppel 2006). Cladonomy (the naming of clades) practiced by cladists is not in itself incompatible with the existence of a parallel evolutionary classification. It becomes only so when cladists name their clades by reusing the nomina previously associated to taxa! It is understandable for example that cladists want to name the clade comprising bony fishes and tetrapods, but it is quite indefensible that they use for this the term Osteichthyes by claiming that bony fishes are paraphyletic (Brummitt 2006). However the use of a new word like euteleostomi avoids the unnecessary competition between clades and taxa for the same nomina. Similarly it would be incongruous to redefine the term Reptilia to encompass all amniotes.

The problem today is that the nomenclature is torn between three distinct codes for historical reasons, separately addressing zoology (Ride et al. 1999), botany (McNeill et al. 2012) and bacteriology (Lapage et al. 1992). This separation is frankly outdated and leads to fantastic nonsense,

such as the fact that a taxon may be treated by two competing codes and therefore receives two distinct scientific names (for example the phylum Euglenozoa = the division Euglenophyta, or the dinoflagellate class Syndinea = Syndiniophyceae) or else that some taxa may be formally treated by no code (for example bacterial taxa above the rank of class). This is why it is urgent that systematists finally endow a single nomenclatural code replacing the current three. This code should not be a simple synthesis of those old codes like the current draft *BioCode* (Greuter et al. 2011), but will have to embody a radical renovation of biological nomenclature assigning a special status to three types of groups: taxa, clades and grades. It is necessary to understand that these three concepts are not exclusive (Cavalier-Smith 1998), and that a biological group can, without contradiction, belong to zero, one, two or three of these categories. I therefore suggest the integration of the 8 following proposals to the next BioCode:

1. The recognition in preamble of the existence of three types of groups governed by the rules of the *BioCode*: taxa, clades and grades. This however is not the role of nomenclature to assign them a precise formal definition. For the sake of simplicity, scientific names of these groups should always be treated in local languages as proper nouns in the singular (even if their Latin number is plural). Example: "Plantae is a taxon" (notice the use of singular whereas *plantae* is a Latin plural).
2. Taxa are hierarchized within a *phylogenetic classification* (adjectives like "traditional" or "classical" should be avoided because they are often pejorative and have ideological connotations). They have a taxonomic rank that can be as high as empire (imperium) and as low as subvariety (subvarietas).
3. Clades do not have ranks (this should appeal to the original designers of the *PhyloCode*) and are nested within a *phyletic arrangement*. Some cladists who have examined this issue have agreed that their way of arranging organisms does not result in a classification *sensu stricto* (Griffiths 1974) and that cladograms were not genealogies (and therefore not phylogenies).
4. In order to visually distinguish microtaxonomy and macrotaxonomy, taxa of rank lower than or equal to genus must be written in italics, while those of rank strictly higher must be written in roman (upright). Examples: Mammalia (class), *Caenorhabditis* (genus).
5. If the delimitation of a clade or a grade does not match that of a taxon, it is necessary to coin a new name if one wants to formally designate this group. The use of a synapomorphy is usually seen as the best way to define a clade.
6. In order not to confuse on the one hand taxa, and on the other hand clades and grades that are not taxa (although clades and grades can be taxa), these latter shall neither be capitalized (which is unique to taxa of rank strictly higher than species) nor be written in italics (which should be specific to taxa of rank lower than or equal to genus) and their ending should not match a categorical suffix (like "-phyta", "-ales", "-idea" etc.). Examples: neomura, opisthokonta, corticata, euteleostomi, amniota, streptobionta.
7. The desire for taxonomic stability should be reaffirmed by explicitly prohibiting the use of paraphyly (or even simple heteroclady) as a pretext to change the delimitation of a taxon. It is an irrelevant criterion.
8. To facilitate the identification of paraphyletic groups, which are unsuitable for a phyletic arrangement or a cladistic analysis, they should always be followed by an asterisk if paraphyly is believed to be sufficiently proven (even if it is a cryptic one, as in the case of choanoflagellates). Examples: Osteichthyes*, Choanoflagellata*, Biliphyta* (paraphyletic taxa); pisces*, eubacteria* (grades that are neither taxa nor clades).

It has been proposed to exclude polyphyletic groups from the notion of grade (Willner et al. 2014), which may be relevant given that there is already a term, the word "phenon," that refers to overall similarity without any consideration for phylogeny. I am not sure, however, that this distinction truly has its place in the *BioCode*; that is why I have not included it in the above

suggestions, despite its merits. These few proposals, although quite drastic, nevertheless fit a continuation of nomenclatural tradition in seeking to promote stability, universality and flexibility. When cladism emerged, its advocates have criticized classical taxonomy for its authoritarianism. Cladists would therefore betray their noble ideals of freedom and transparency if they were going to continue to impose their recurring redefinitions of paraphyletic taxa to the rest of the scientific community. All of these 8 suggestions can be applied right now without waiting for a potential future integration to the *BioCode* since they do not contradict any of the rules of the current codes.

By following these proposals, cladists would be entirely free to continue to consider that only clades are natural, while evolutionists could freely think in terms of taxa without their definitions being modified each time that a study shows that they are paraphyletic: it would be sufficient to add an asterisk. Cladists would immediately know when reading an evolutionist paper that groups with an asterisk do not fundamentally interest them. Conversely, evolutionists would also know when reading a cladist paper that groups whose names are not capitalized (and not in italics) are not natural regarding their views. There would be no longer terminological dispute between the two schools, and both would be able to freely arguing about the merits and shortcomings of their respective philosophies and their scientific results. This is possible because, while divergent on formal classification, both schools have converged on the subject of phylogenetic inference (Stuessy 2013). Museums, conservation biologists, authors of textbooks and books, etc. would also be free to choose between *phylogenetic classification* and *phyletic arrangement*, the one deemed as the most appropriate to their practice or presentation of their comments. It would be foolish to refuse to turn the frontal opposition between cladists and evolutionists and the competition between clades and taxa for the same nomina, which has considerably hampered the progress of science for decades, into a mutually beneficial cooperation.

ACKNOWLEDGMENTS

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ANNEXE: MATHEMATICAL PROOFS

Lemma 1.5:

The individual a being an ancestor of b, there exists a lineage $x_1, x_2, \ldots, x_n$ such that $n > 1$, $x_1 = a$, $x_n = b$, and $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq n - 1$.

Likewise, b being an ancestor of c, there exists a lineage $x_n, x_{n+1}, \ldots, x_k$ such that $k > n$, $x_n = b$, $x_k = c$, and $(x_i, x_{i+1}) \in p$ for every i, $n \leq i \leq k - 1$.

It exists therefore a sequence $x_1, x_2, \ldots, x_k$ such that $k > 2$, $x_1 = a$, $x_k = c$, and $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq k$. Thus, according to Definition 1.3, a is an ancestor of c. □

Lemma 1.6:

Let there be x and y such that $x \neq y$ and y is an ancestor of x. By definition, it exists a lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = y$, $x_n = x$ and, since $n \geq 2$, then $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq n - 1$.

If we assume that x is an ancestor of y, then it exists a sequence $x_n, x_{n+1}, \ldots, x_k$ such that $x_n = x$, $x_k = y$ and, since $k > n$, then $(x_i, x_{i+1}) \in p$ for every i, $n \leq i \leq k - 1$. It exists therefore a lineage $x_1, x_2, \ldots, x_k$ such that $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq k - 1$. Yet $y = x_1 = x_k$ which is contradictory with the acyclicity of p. Therefore x cannot be an ancestor of y. □

Lemma 1.7:

Let there be $x \notin g$ such that a is an ancestor of x, then according to Definition 2.3 it exists a lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$, $x_n = x$, and $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq n - 1$.

Let there be the proposition $\mathcal{P}(i)$ = "$x_i \in g$". We know that $\mathcal{P}(1)$ is true because $x_1 = a$ which belongs to g. Let there be the proposition $\mathcal{Q}$ = "it exists a pair $(x_i, x_{i+1}) \in p$ such that $x_i \in g$ and $x_{i+1} \notin g$". Now let us assume that $\mathcal{Q}$ is false, then for every pair $(x_i, x_{i+1}) \in p$, $x_i \notin g$ or $x_{i+1} \in g$.

If it is assumed that $\mathcal{P}(i)$ is true, then clearly $x_{i+1} \in g$, so $\mathcal{P}(i+1)$ is true. We deduce by the recurrence theorem that $\mathcal{P}(i)$ is true for every i, $1 \leq i \leq n$. Yet we know that $\mathcal{P}(n)$ is false since $x_n = x$ which does not belong to g. We conclude from this contradiction that $\mathcal{Q}$ cannot be false. □

Lemma 1.11:

Let us assume the existence of a second lineage $y_1, y_2, \ldots, y_k$ such that $y_1 = a$ et $y_k = x$. Let there be the proposition $\mathcal{P}(i)$ = "$x_{n-i} = y_{k-i}$" defined for every i, $0 \leq i \leq \min(n, k) - 1$.

Since $y_k = x_n = x$, it is clear that $\mathcal{P}(0)$ is true. Now let us assume that $\mathcal{P}(i)$ is true for a certain $i < \min(n, k) - 1$. Then, the network G being without mergings, it exists only one individual $z \in X$ such that $(z, x_{n-i}) \in p$, and since $x_{n-i} = y_{k-i}$ we also know that $(z, y_{k-i}) \in p$. Yet, it already exists x_{n-i-1} and y_{k-i-1} such that $(x_{n-i-1}, x_{n-i}) \in p$ and $(y_{k-i-1}, y_{k-i}) \in p$, which allows us to assert that $z = x_{n-i-1} = y_{k-i-1}$, and therefore that $\mathcal{P}(i+1)$ is true. We deduce by the recurrence theorem that $\mathcal{P}(i)$ is true for every i, $0 \leq i \leq \min(n, k) - 1$.

If we now assume that $n > k$, then $\mathcal{P}(k\text{-}1)$ = "$x_{n-k+1} = y_1$" is true. Yet, since $y_1 = x_1 = a$ then it must exist a lineage $x_1, \ldots, x_{n-k+1}$ such that $x_1 = x_{n-k+1} = a$, which is contradictory with the acyclicity of p by Definition 1.1. The same reasoning symmetrically applies if we conversely assume that $k > n$, forcing us to conclude that $k = n$. The lineage that connects x to its ancestor a is therefore unique. □

Theorem 1.12:

Let there be a genealogical network $G = (X, p)$ without mergings and the individuals $a, b, x, y \in X$ such that a is an ancestor of x and y, and b is an ancestor of x but not of y. By Lemma 2.11, it exists three unique lineages $(x_i)_{1 \leq i \leq n}$, $(x'_i)_{1 \leq i \leq p}$, and $(x''_i)_{1 \leq i \leq q}$ such that $x_1 = x'_1 = a$, $x''_1 = b$, $x_n = x''_q = x$ and $x'_p = y$.

Let there be the proposition $\mathcal{P}(i)$ = "$x_{n-i} = x''_{q-i}$" defined for i such that $0 \leq i \leq \min(n, q) - 1$. $\mathcal{P}(0)$ is trivially true. Let us now assume that $\mathcal{P}(i)$ is true for a certain $i < \min(n, q) - 1$. We know by definition that $(x_{n-(i+1)}, x_{n-i}) \in p$ and also that $(x''_{q-(i+1)}, x''_{q-i}) \in p$. Yet, G being a network without mergings, we can deduce that $x_{n-(i+1)} = x''_{q-(i+1)}$ and therefore that $\mathcal{P}(i+1)$ is true. By the recurrence theorem $\mathcal{P}(i)$ is therefore true for every i.

Let us now assume that $q \geq n$, then $\mathcal{P}(n\text{-}1)$ = "$x_1 = x''_{q-(n-1)}$", hence $x''_{q-(n-1)} = a$. Yet, b being an ancestor of $x''_{q-(n-1)}$, we deduce that b is an ancestor of a. The individual a, being itself an ancestor of y, we deduce that b is an ancestor of y, which is absurd. We are thus forced to conclude that $n > q$. In this case we know that $\mathcal{P}(q\text{-}1)$ = "$x_{n-(q-1)} = x''_1$". Yet $x''_1 = b$, and $x_1 = a$ is an ancestor of $x_{n-(q-1)}$, therefore a is an ancestor of b. □

Lemma 2.4:

Let there be a monophyletic group g and $a \in g$ a common ancestor of g. Let us assume that there exists an individual $a' \neq a$ such that $a' \in g$ and a' is a common ancestor of g. Since $a \in g$ then a' is an ancestor of a. By Lemma 1.6, a is not an ancestor of a'. But symmetrically, since $a' \in g$ and a is a common ancestor of g, then a is an ancestor of a', which is contradictory. A monophyletic group can therefore include only one common ancestor. Let us now assume that a is not a most recent common ancestor (cenancestor) of g, then there must exist another common ancestor a'' of g such that a is an ancestor of a''. However because $a \in g$, we must conclude that a'' is also an ancestor of a, which is again impossible by Lemma 1.6. □

Lemma 2.6:

The group g being continuous, it exists by Definition 2.5 at least one lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$, $x_n = x$ and $x_i \in g$ for every i, $1 \leq i \leq n$. By Lemma 1.11 there does not exist in X a second lineage $x'_1, x'_2, \ldots, x'_n$ such that $x'_1 = a$ and $x'_n = x$. □

Lemma 2.7:

Let us assume there exist two distinct individuals $a, a' \in X$ most recent common ancestors of g. There exist therefore $x \in g$ such that a and a' are ancestors of x. The network G being without mergings, a being an ancestor of itself, and a' being not an ancestor of a by Definition 2.2, we must conclude by Theorem 1.12 that a is an ancestor of a', which is impossible. □

Lemma 3.5:

Let us name a_2 and a_3 respectively the included common ancestors of g_2 and g_3. The group g_2 being ancestral to g_3, there exist an individual $x_2 \in g_2$ such that x_2 is an ancestor of a_3. Since $x_2 \in g_2$, a_2 is an ancestor of x_2. The group g_1 being ancestral to g_2, there exist an individual $x_1 \in g_1$ such that x_1 is an ancestor of a_2. By Lemma 1.5, x_1 is an ancestor of a_3, therefore g_1 is ancestral to g_3. □

Theorem 3.6:

($\Leftarrow$) Let there be g_1 and g_2 two monophyletic groups such that g_1 is ancestral to g_2 and $g_1 \cap g_2 = \emptyset$. Let also be $g = g_1 \cup g_2$. Let us name a_1 the unique included common ancestor of g_1, and a_2 the one of g_2. There exists by definition a certain $x \in g_1$ such that x is an ancestor of a_2.

For every $y \in g$, $y \in g_1$ or else $y \in g_2$. In the first case, a_1 is by definition an ancestor of y. In the second case, we know that a_1 is an ancestor of x, that x is an ancestor of a_2, and that a_2 is an ancestor of y. By Lemma 1.5, we deduce that a_1 is an ancestor of y. The individual a_1 is therefore the unique included common ancestor of g. This group is therefore monophyletic. The reasoning is symmetrical if we would have chosen that g_2 is ancestral to g_1.

($\Rightarrow$) Let there be g_1 and g_2 two monophyletic groups such that $g_1 \cap g_2 = \emptyset$. Let also be $g = g_1 \cup g_2$ a monophyletic group. Let us name a_1, a_2, and a the respective included common ancestors of g_1, g_2 and g. Then, either $a \in g_1$ or $a \in g_2$. Let us choose $a \in g_1$. We know by definition that a is an ancestor of x for every $x \in g$. In particular $a_2 \in g$, so a is an ancestor of a_2. Therefore g_1 is ancestral to g_2. Symmetrically if we would have chosen $a \in g_2$, we would then have to conclude that a is an ancestor of a_1 and therefore that g_2 is ancestral to g_1. □

Theorem 3.7:

($\Leftarrow$) Let there be g_1 and g_2 two continuous groups such that g_1 is directly ancestral to g_2 (again, g_1 and g_2 have symmetrical roles), and $g = g_1 \cup g_2$. Let us name a_1 the unique included common ancestor of g_1 and a_2 the unique included common ancestor of g_2.

For every $y \in g$, either $y \in g_1$ or $y \in g_2$. If $y \in g_1$ then, since g_1 is continuous, it exists a lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$, $x_n = x$, and if $n > 1$ then for every i, $1 \leq i \leq n - 1$, $x_i \in g_1 \subset g$ and $(x_i, x_{i+1}) \in p$.

Conversely, let us now consider the case $y \in g_2$. The group g_1 being directly ancestral to g_2, it exists a certain $x \in g_1$ such that $(x, a_2) \in p$. The group g_1 being continuous, there exists a lineage $x_1, x_2, \ldots, x_m$ such that $x_1 = a_1$, $x_m = x$, and if $m > 1$ then for every i, $1 \leq i \leq m - 1$, $x_i \in g_1 \subset g$ and $(x_i, x_{i+1}) \in p$. Since g_2 is continuous, it exists a lineage $x_{m+1}, x_{m+2}, \ldots, x_n$ such that $x_{m+1} = a_2$, $x_n = y$, and if $n - m > 1$ then for every i, $m + 1 \leq i \leq n - 1$, $x_i \in g_2 \subset g$ and $(x_i, x_{i+1}) \in p$. We thus deduce that for every $y \in g_2$ it exists a sequence $x_1, x_2, \ldots, x_{m+n}$ such that $x_1 = a_1$, $x_{m+n} = y$, and since $m + n > 1$ then for every i, $1 \leq i \leq m + n - 1$, it is true that $x_i \in g$ and $(x_i, x_{i+1}) \in p$. The group g is therefore continuous.

($\Rightarrow$) Let there be g_1 and g_2 two continuous groups such that $g_1 \cap g_2 = \emptyset$. Let there be also the continuous group $g = g_1 \cup g_2$. Let us name a the unique included common ancestor of g. For every

$x \in g$, either $x \in g_1$ or $x \in g_2$. Let us assume that $a \in g_1$ (the reasoning is symmetrical if we choose $a \in g_2$).

By definition, for every $y \in g$ it exists a lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$, $x_n = y$, and if $n \geq 2$ then $x_i \in g$ and $(x_i, x_{i+1}) \in p$ for every i, $1 \leq i \leq n - 1$. Let us choose $y \in g_2$.

Let there be the simple proposition $\mathcal{P}(i)$ = "$x_i \in g_1$". We know that $\mathcal{P}(1)$ is true because $x_1 = a \in g_1$. Let there be the proposition $\mathcal{Q}$ = "it exists a pair $(x_i, x_{i+1}) \in p$ such that $x_i \in g_1$ and $x_{i+1} \in g_2$."

Let us assume that $\mathcal{Q}$ is false, then for every pair $(x_i, x_{i+1}) \in p$ of this lineage, $x_i \in g_2$ or $x_{i+1} \in g_1$. If we assume that $\mathcal{P}(i)$ is true then clearly $x_i \notin g_2$, so $x_{i+1} \in g_1$, therefore $\mathcal{P}(i+1)$ is true. We deduce by the recurrence theorem that $\mathcal{P}(i)$ is true for every i, $1 \leq i \leq n$. However, we know that $\mathcal{P}(n)$ is false since $x_n = y \notin g_1$. We deduce from this contradiction that $\mathcal{Q}$ cannot be false.

Let us name (x, x') one such of these pairs, so that $x \in g_1$ and $x' \in g_2$. Let us consider the case $y = a_2$, since x' belongs to the lineage leading to y, then x' is an ancestor of a_2. But since $x' \in g_2$ we know that a_2 is also an ancestor of x'. We deduce by Lemma 1.6 that $a_2 = x'$. It exists therefore a certain $x \in g_1$ such that $(x, a_2) \in p$. Thus, the group g_1 is directly ancestral to g_2. □

Lemma 4.3:

Let there be a monophyletic group g and a its (included) cenancestor.

($\Rightarrow$) If g is paraphyletic, then there exists by definition a pair $(b, x) \in p$ such that $b \in g$ and $x \notin g$. The individual a is an ancestor of b since $b \in g$, so by Lemma 1.6, a is an ancestor of $x \notin g$.

If g is holophyletic, then by definition there does not exist a pair $(b, x) \in p$ such that $b \in g$ and $x \notin g$. But let us assume that there exists $y \notin g$ such that a is an ancestor of y. Then by Lemma 1.7 for every lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a$ and $x_n = y$, it exists a certain i, $1 \leq i \leq n - 1$, such that $x_i \in g$ and $x_{i+1} \notin g$. This clearly contradicts the definition of holophyly, therefore it does not exist $y \notin g$ such that a is an ancestor of y.

($\Leftarrow$) Let there be $x \notin g$ such that a is an ancestor of x, then by Lemma 1.7 for every lineage x_1, $x_2, \ldots, x_n$ such that $x_1 = a$ and $x_n = x$, it exists a certain i, $1 \leq i \leq n - 1$, such that $x_i \in g$ and $x_{i+1} \notin g$. The group g is therefore paraphyletic.

Conversely, let us assume that for every $y \in X$, if a is an ancestor of y then $y \in g$. But let us also assume that there exists a pair $(x, y) \in p$ such that $x \in g$ and $y \notin g$. Since $x \in g$, a is an ancestor of x, which is an ancestor of y. So by Lemma 1.5, a is an ancestor of $y \notin g$. This is clearly contradictory, therefore it does not exist any pair $(x, y) \in p$ such that $x \in g$ and $y \notin g$, so g is holophyletic. □

Lemma 4.6:

Let there be a group g and $A \neq \emptyset$ the set of all the most recent common ancestors of g.

($\Rightarrow$) If g is heterophyletic then for every $a \in A$, there exists $x \in X$ such that a is an ancestor of x and $x \notin g$. Let us assume that there exists $a \in A$ such that $a \in g$ then by Lemma 2.4, a is the unique included common ancestor of a. Thus, it exists $x \in X$ such that a is an ancestor of x and $x \notin g$, therefore by Lemma 4.3, g is paraphyletic. Conversely, let us now assume that $a \notin g$ for every $a \in A$, then by Definition 4.4, g is polyphyletic.

($\Leftarrow$) If g is paraphyletic then by Lemma 2.4 it exists exactly one $a \in A$ such that $a \in g$. By Lemma 4.3, it exists $x \notin g$ such that a is an ancestor of x. The group g is thus heterophyletic.

If g is polyphyletic then $a \notin g$ for every $a \in A$. Yet, for every $a \in A$, a is a trivial ancestor of a. We deduce from this that g is heterophyletic. □

Lemma 5.2:

Let there be a group g whose elements are called $x_1, x_2, \ldots, x_n$. The set $\{\{x_1\}, \{x_2\}, \ldots, \{x_n\}\}$ is a continuous partition of g since firstly for every i, $1 \leq i \leq n$, $\{x_i\} \neq \emptyset$ and $\{x_i\}$ is a trivial continuous group; secondly if $n \geq 2$ then for every i, j, $1 \leq i < j \leq n$, $\{x_i\} \cap \{x_j\} = \emptyset$; and thirdly $\bigcup_{1 \leq i \leq n} \{x_i\} = g$.

Let us now assume that there exists a continuous partition $\{g_1, g_2, \ldots, g_k\}$ having a number of elements k strictly superior to n, the number of elements of g. For every i, $1 \leq i \leq n$, $g_i \neq \emptyset$, therefore $\text{card}(g_i) \geq 1$. Since for every i, j, $1 \leq i < j \leq k$, $g_i \cap g_j = \emptyset$, we have $\text{card}(\bigcup_{1 \leq i \leq k} g_i) \geq k$. Yet, $\bigcup_{1 \leq i \leq k} g_i = g$ and $\text{card}(g) = n < k$. From this contradiction we conclude that there does not exist a continuous partition having a number of elements strictly superior to the number of elements of g. □

Theorem 5.4:

Let us name a the unique included common ancestor of g. Then it exists a certain i, $1 \leq i \leq n$, such that $a \in g_i$. For every $j \neq i$, $1 \leq j \leq n$, and for every $x \in g_j$ we know that a is an ancestor of x since $x \in g$. Yet $x \notin g_i$, therefore by Lemma 4.3 we conclude that g_i is paraphyletic. □

Theorem 5.7:

Let us assume that there exists a continuous partition $K' = \{g'_1, g'_2, \ldots, g'_n\}$ such that $\text{card}(K') = n$ and $K \neq K'$. That is to say, there exists at least one i, $1 \leq i \leq n$, such that for every j, $1 \leq j \leq n$, $g_i \neq g'_j$. Let there be such a group g_i, and let us name a_i the unique included common ancestor of g_i. There exists a certain j, $1 \leq j \leq n$, such that $a_i \in g'_j$. We know by definition that $g_i \neq g'_j$ therefore it exists a certain $x \neq a_i$ such that $x \in g_i$ and $x \notin g'_j$ or else $x \notin g_i$ and $x \in g'_j$.

The reasoning is symmetrical in both cases. Let us assume that $x \in g_i$ and $x \notin g'_j$, then by Lemma 1.7, there exists a lineage $x_1, x_2, \ldots, x_n$ such that $x_1 = a_i$, $x_n = x$, and also a certain u, with $1 \leq u \leq n - 1$, such that $x_u \in g'_j$ and $x_{u+1} \notin g'_j$. The group g_i being continuous and without mergings, then by Lemma 2.6 this lineage is unique. Since $a_i \in g_i$, $x \in g_i$, and g_i is continuous, then by Definition 2.5, for every u, $1 \leq u \leq n$, $x_u \in g_i$. As a result, it exists $b, c \in g_i$ such that $(b, c) \in p$, $b \in g'_j$ and $c \notin g'_j$.

Now let us name g'_k the group of K' such that $c \in g'_k$ and a'_k the unique included common ancestor of g'_k. The individual a'_k is therefore an ancestor of c, and it exists a lineage $x'_1, x'_2, \ldots, x'_m$ such that $x'_1 = a'_k$, $x'_m = c$ and for every u, $1 \leq u \leq m$, $x'_u \in g'_k$. It we assume that $m \geq 2$, then the group g'_k being without mergings, it exists a unique x'_{m-1} such that $(x'_{m-1}, x'_m) \in p$. We know that $(b, x'_m) \in p$ therefore $b = x'_{m-1}$. Yet $b \notin g'_k$ although $x'_{m-1} \in g'_k$. We deduce from this contradiction that $m = 1$, therefore $c = a'_k$. The group g'_j is consequently directly ancestral to g'_k. By Theorem 3.7, the union $g'_j \cup g'_k$ is a continuous group. Therefore it exists a continuous partition K'' of g with cardinal $n - 1$, which contradicts the premise. Thus, we must conclude that there does not exist a continuous partition K' of g such that $\text{card}(K') = n$ and $K \neq K'$. □

Theorem 6.2:

It is clear by Lemma 5.2 that any genealogical network can be transformed into a phylogenetic network. To show that these two types of networks are in fact the same, it is enough to show that p' is acyclic like p.

Let there be a sequence of continuous groups $g_1, g_2, \ldots, g_n$ such that $n \geq 2$ and $(g_i, g_{i+1}) \in p'$ for every i, $1 \leq i \leq n - 1$. By Lemma 3.5, g_1 is ancestral to g_n. Let us name a_1 and a_n the respective cenancestors of g_1 and g_n. Then it exists a certain $x \in g_1$ such that x is an ancestor of a_n. Since $x \in g_1$, then we know that a_1 is an ancestor of x, so by Lemma 1.5 a_1 is an ancestor of a_n.

Let us now assume that $g_1 = g_n$. Then $a_1 = a_n$. Therefore it exists a lineage $x_1, x_2, \ldots, x_n$ such that $a_1 = x_1 = x_n = a_n$. This contradicts the fact that p is acyclic on X. Since it is consequently impossible that $g_1 = g_n$, then p' must be acyclic on X'. □

Lemma 7.5:

Let there be a the unique included common ancestor of g'. Then we know that a is a common ancestor of g. For every $x \in g$, a is therefore an ancestor of x. By Lemma 4.3, g' is not holophyletic if $x \notin g'$, therefore we deduce that for every $x \in g$ we have $x \in g'$, so $g \subset g'$. The converse is false since we know that it is possible that $a \notin g$. □

Lemma 7.11:

Since g^* is monophyletic here, then there exists by Lemma 3.4 a unique common ancestor of g^* called a^*. Let us assume that $a^* \in A^*$, then there exists a certain $g'_h \in H$ such that a^* is the included common ancestor of g'_h, therefore $g^* \subset g'_h$, which means that for any $x \in g^*$ we know that $x \in g'_h$. Yet, by definition for every $x \in g^*$ we know that $x \notin g'_k$, so we deduce that $g'_h \cap g'_k = \emptyset$. Yet by Lemma 7.5, $g \subset g'_h$ and $g \subset g'_k$, therefore $g = \emptyset$, which is absurd. Thus, it is impossible that $a^* \in A^*$. □

Lemma 7.12:

Let there be g a clade in K, a an exclusive and most recent common ancestor of g, g' a canonical holophyletic group of g such that a is the unique included common ancestor of g', g'' the non-empty basal group of g relatively to g'.

By definition a is the unique included common ancestor of g'', thus making it a monophyletic group. By Observation 7.9, there exists a certain $x \in g$ such that $x \notin g''$. Yet, for any $x \in g$, a is an ancestor of x, therefore g'' is paraphyletic. □

Lemma 7.13:

Let there be g a clade in K, A the set of all the common ancestors of g, A' the set of all the exclusive common ancestors of g in K, $H = \{g'_1, g'_2, \ldots, g'_n\}$ the set of all the holophyletic groups canonically associated to g, and g^* a stem-group of g relatively to a certain $g'_k \in H$ whose cenancestor is also a cenancestor of g. Let us name a'_i the included common ancestors of g'_i.

If the set of all the common ancestors of g^* is empty then by Definition 4.4 g^* is polyphyletic and therefore heterophyletic. Now let us assume that a^*, a common ancestor of g^*, exists. Then a^* is an ancestor of at least some a'_i, which are all ancestors of every $x \in g$. By Lemma 1.5 a^* is therefore an ancestor of every $x \in g$. By Lemma 7.5, $g \subset g'_i$ for every i, $1 \leq i \leq n$. Yet by definition for every $x \in g'_k$ we know that $x \notin g^*$, thus $g^* \cap g = \emptyset$. Therefore it exists a certain $x \notin g^*$ such that a^* is an ancestor of x. So by Definition 4.5 g^* is heterophyletic, and more precisely paraphyletic if $a^* \in g^*$. □

Theorem 8.3:

Let there be g a clade in K and the set $\{g_1, g_2\}$ a cladistic partition of g. Let us assume that there exists a second cladistic partition $\{g_3, g_4\}$. Let there be a_1, a_2, a_3 and a_4 the exclusive common ancestors of respectively g_1, g_2, g_3 and g_4. Whatever $x \in g$ we know that $x \in g_1$ or else $x \in g_2$, and also $x \in g_3$ or else $x \in g_4$. If we assume that $g_1 \neq g_3$ (and $g_1 \neq g_4$), then there exist $x, y \in g_1$ (or else $x, y \in g_2$) such that $x \in g_3$ and $y \in g_4$.

In the first case this means that a_1 (or else a_2) is an ancestor of x and y, and that a_3 is an ancestor of x but not of y. Since the network is without mergings then we can deduce by Lemma 1.11 that a_1 (or else a_2) is an ancestor of a_3. Symmetrically, a_1 (or else a_2) is an ancestor of x and y whereas a_4 is an ancestor of y but not of x, which implies in the same way that a_1 (or else a_2) is an ancestor of a_4. Therefore for every $x \in g_3$ we have $x \in g_1$, and also for every $x \in g_4$ we have $x \in g_1$. Yet, since $g_3 \cup g_4 = g$, then for every $x \in g$ we have $x \in g_1$. There exists therefore no $x \in g$ such that $x \in g_2$, so $g_2 = \emptyset$, which is absurd. □

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